



# Unraveling the influences of climate change in Lepidosauria (Reptilia)

Luisa Maria Diele-Viegas\*, Carlos Frederico Duarte Rocha

Departamento de Ecologia, Universidade do Estado do Rio de Janeiro, Rio de Janeiro, Brazil

## ARTICLE INFO

### Keywords:

Squamata  
Rhynchocephalia  
Climate change  
Review  
Thermal biology  
Genetics  
Reproductive biology  
Behavior  
Species distributions

## ABSTRACT

In recent decades, changes in climate have caused impacts on natural and human systems on all continents and across the oceans and many species have shifted their geographic ranges, seasonal activities, migration patterns, abundances and interactions in response to these changes. Projections of future climate change are uncertain, but the Earth's warming is likely to exceed 4.8 °C by the end of 21st century. The vulnerability of a population, species, group or system due to climate change is a function of impact of the changes on the evaluated system (exposure and sensitivity) and adaptive capacity as a response to this impact, and the relationship between these elements will determine the degree of species vulnerability. Predicting the potential future risks to biodiversity caused by climate change has become an extremely active field of research, and several studies in the last two decades had focused on determining possible impacts of climate change on Lepidosaurians, at a global, regional and local level. Here we conducted a systematic review of published studies in order to seek to what extent the accumulated knowledge currently allow us to identify potential trends or patterns regarding climate change effects on lizards, snakes, amphisbaenians and tuatara. We conducted a literature search among online literature databases/catalogues and recorded 255 studies addressing the influence of climate change on a total of 1918 species among 49 Lepidosaurian's families. The first study addressing this subject is dated 1999. Most of the studies focused on species distribution, followed by thermal biology, reproductive biology, behavior and genetics. We concluded that an integrative approach including most of these characteristics and also bioclimatic and environmental variables, may lead to consistent and truly effective strategies for species conservation, aiming to buffer the climate change effects on this group of reptiles.

## 1. Introduction

### 1.1. Climate changes

Climate change is defined as any change in the mean and/or variability of climate properties that persist for an extended period, caused by natural processes or anthropogenic changes in atmosphere composition and land use (Cubasch et al., 2013). During the Quaternary (2.58 Ma to present), the climatic fluctuations have promoted worldwide consequences for past and present-day biota (Fordham et al., 2017). The rapid and extreme climatic fluctuations associated with environmental shifts were important factors promoting the extinction of many lineages (Cooper et al., 2015). However, the importance of climate-change velocity for a group depends on its dispersal abilities (Sandel et al., 2011), since meta-population structures and processes were involved in maintaining ecosystem stability during the repeated phases of sudden climate changes (Cooper et al., 2015).

Velocity of past climate change is also related to endemism patterns for several groups, such as for Tetrapoda (Araujo et al., 2008;

Sandel et al., 2011). High velocity was associated with larger median and lower variation in range size within assemblages, while low velocity was associated with high endemism and low dispersion capacity (Sandel et al., 2011). For herptiles, current distributions of widespread species are more constrained by current climate changes, while the distribution of narrow ranging species is markedly constrained by past climate conditions (Jansson, 2003). Thus, narrow-ranging species are at least partly restricted because of their poor ability to track current climate changes (Jansson, 2003).

The dominant cause of long-term Cenozoic climate trends, as in other geological eras, was the total amount of Carbon dioxide (CO<sub>2</sub>) in atmosphere, ocean, soil and biosphere, which changes over millions of years due to imbalance of the volcanic source and weathering sink (Hansen and Sato, 2012). Since the pre-industrial era, anthropogenic greenhouse gas emissions have exponentially increased due to economic and population growth (Stocker et al., 2013). This lead to an accelerated replication of natural patterns, which may have been the dominant cause of the increase of Earth's mean air temperature of 0.85 °C in the last 100 years (Cubasch et al., 2013; Hartmann et al.,

\* Corresponding author.

E-mail address: [luisa.mviegas@gmail.com](mailto:luisa.mviegas@gmail.com) (L.M. Diele-Viegas).

<https://doi.org/10.1016/j.jtherbio.2018.11.005>

Received 3 April 2018; Received in revised form 25 October 2018; Accepted 12 November 2018

Available online 15 November 2018

0306-4565/ © 2018 Elsevier Ltd. All rights reserved.

2013).

Projections of future climate change are uncertain due to the lack of the climate system understanding and the existence of internal climate variability (Collins et al., 2013). In spite of these limitations, the models simulate many climate aspects with a certain degree of robustness (Flato et al., 2013), and predicts that warming is likely to exceed up to 4.8 °C by the end of 21st century (Collins et al., 2013). The models also predicted an increase in annual mean precipitation in high latitudes and equatorial Pacific, while it will likely decrease in mid-latitude and subtropical dry regions (Collins et al., 2013).

## 1.2. Organismal vulnerability

Changes in climate have caused impacts on natural and human systems all over the World in the recent decades (Pincebourde et al., 2016). Predicting the potential future risks to biodiversity caused by climate change has become an extremely active field of research (Bellard et al., 2012), and some studies suggest that climate change could be the greatest global threat to biodiversity over the next few decades (Leadley et al., 2010; Cahill et al., 2013). The vulnerability to climate change is determined by the interaction between the magnitude and rate of changes to which the system is exposed, its sensitivity to these changes, and the degree to which the system can respond to these changes (Dawson et al., 2011).

Shifts in several biological aspects have been observed in many species and regions (e.g., McCarty, 2001; Peñuelas et al., 2013). These aspects, such as ecological interactions and primary production, are important to delimit the climate impacts on species' functioning and the species' vulnerability to climate change (e.g., Tylianakis et al., 2008; Seddon et al., 2016; Fig. 1). The species responses, in turn, are mainly driven by genotypic adaptation, phenotypic plasticity and the ability to move to thermally suitable habitats (Dawson et al., 2011; Bellard et al., 2012). If none of these are possible, the species are likely to go locally or globally extinct (Sinervo et al., 2010), as happened with the Costa Rican golden toad *Bufo perigrinus* (Pounds et al., 1999) and the Australian melomys *Melomys rubicola* (Gynther et al., 2016).

Genotypic adaptation can occur in very few generations, so species with fast life cycles may have greater response capacity (Settele et al., 2014). High phenotypic plasticity can greatly improve the odds of adaptation if it has low fitness costs; if the costs are high, this improvement will be modest (Chevin et al., 2010). The migration capacity depends on the rate of migration, which for many species is slower than

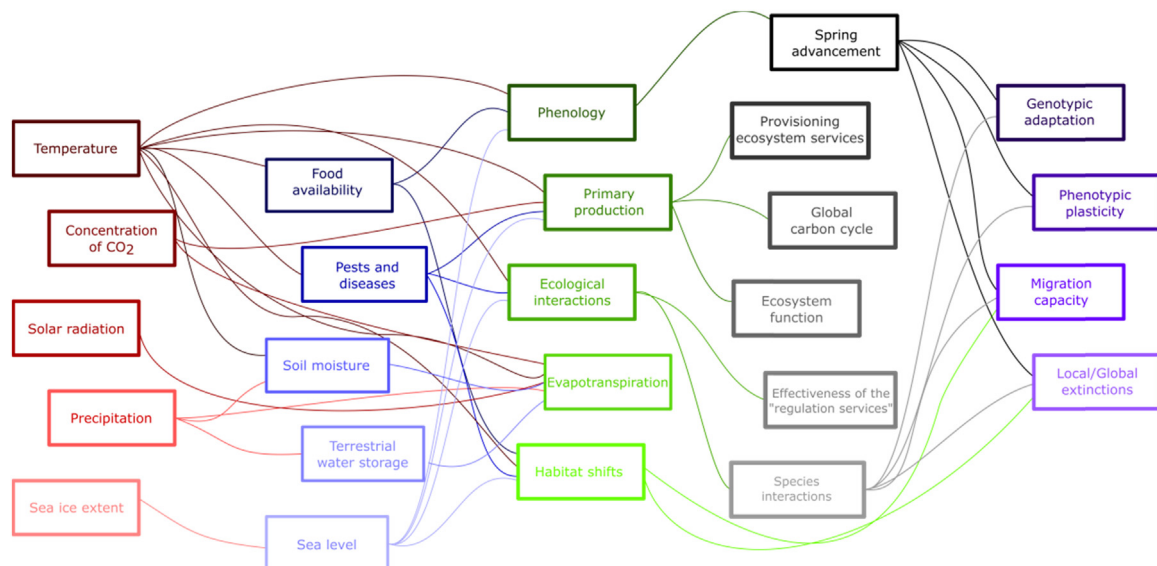
the rate of movement of climate envelopes, ecosystems interactions, and geographical and human barriers (Settele et al., 2014). Therefore, the knowledge about these aspects at species level may be crucial to access their vulnerability to predicted changes (e.g., Huey et al., 2012; Romero-Díaz et al., 2017), thus providing a basis for identifying, proposing and establishing conservation policies.

### 1.2.1. Lepidosauria

Reptiles are among the World's most diverse vertebrates, reaching almost 10,650 species (Uetz et al., 2017). Most are Squamata (lizards, snakes and amphisbaenians, about 10,300 spp.), which together with the one-species sister group Rhynchocephalia form the group Lepidosauria (Uetz et al., 2017). This group shows considerable morphological, physiological and ecological diversity, with most of the species-level diversity occurring in the tropics and sub-tropics (Jetz and Fine, 2012). Some of them, such as the tuatara (Rhynchocephalia), have restricted ranges and rely upon highly-specific environmental conditions, such as rainfall and temperature regimes and/or specific habitats (Meng et al., 2016). Other species have ranges that cover a diversity of climates and must exhibit physiological or behavioral variation to balance thermal budgets between normal daily activities and reproductive demands (Meng et al., 2016).

Due to ectothermy, reptiles are particularly sensitive to changes in environmental temperature and insolation, since their body temperature varies accordingly to the environmental temperature and influences all physiological and behavioral processes (Huey, 1982). The relationship between different aspects of species' thermal physiology, such as preferred temperature, thermal performance and thermal limits, can represent a good measurement to understand the effects of climate change on species' distribution and densities (Sinervo et al., 2010; Kubisch et al., 2016; Diele-Viegas et al., 2018). For example, broad thermal preferences and performance curves may not allow rapid evolutionary response to a quickly warming climate, which can be an indicative of the species vulnerability (Diele-Viegas et al., 2018). Moreover, some species are already experiencing body temperatures above their physiological optima in tropical forests (Huey et al., 2009; Diele-Viegas et al., 2018).

Several studies had focused on determining possible impacts of climate change on reptiles, specifically on Lepidosauria, at a global, regional and local level. Some of them also try to evaluate their adaptive capacity, mostly published in the last decade. Here we conducted a review of these studies aiming to seek to what extent the accumulated



**Fig. 1. Aspects of organismal biology impacted by the climate change.** Climate change components are in red-to-pink, indirect components are in blue, impacted biological aspects are in green, consequences of the impact are in black-to-gray and species' responses to climate change are in purple.

knowledge currently allows us to identify potential trends or patterns regarding climate change effects on lizards, snakes, amphisbaenians and tuatara. Our review highlights several biological characteristics of Lepidosaurians that may be directly influenced by changes in environmental conditions, and the state of the knowledge about the possible responses to this influence. We also seek to answer if the global warming is in fact negatively affecting the Lepidosaurians.

## 2. Methods

### 2.1. Scope of the review

We focused our research on published studies about the influences of current climate changes on Lepidosauria. We conducted a literature search among online literature databases/catalogues (Periódicos CAPES, PubMed, Scholar Google, SciELO, Scopus, Web of Science and Wiley online Library), using the following key words: [Climate Change OR Global Warming OR Climate Warming OR Cambio Climático OR Mudanças Climáticas OR Aquecimento Global] AND [Lizard\* OR Snake\* OR Sphenodon OR Tuatara OR Lepidosauria OR Squamata OR Lagarto\* OR Serpente\*]. We also included studies found during the process of contacting authors and studies listed in the references sections of the articles obtained and that were not captured by the search in the literature databases/catalogues. We excluded studies that focused on paleoclimatic changes, since we are focusing on the effects of current and future climate changes.

We recorded and accessed a total of 255 articles published from 1999 to January 2018, from each we extracted information on the keywords, location of research (by Zoogeographical realms, following Holt et al., 2012), investigated taxonomic level, main subject and impact suffered (negative, neutral or positive; Table S1). We also recovered 969 values of statistical analysis results, among regressions, ANOVA's, chi squares and *t*-tests, and conducted a meta-analysis by using the package metafor (Viechtbauer, 2010) in the statistical software environment R 3.4.3 (R Core Team, 2017). The goal of the meta-analysis was to verify if the current literature agrees statistically with the premise that global warming is in fact affecting the Lepidosauria, being this effect negative, positive or neutral. We converted AUC, *F*, *R*<sup>2</sup>, *T* and  $\chi^2$  values into Pearson's *r* based on Lipsey and Wilson (2001), Borenstein et al. (2011), Lane (2018) and Salgado (2018). Then, we calculated the mean *r* by evaluated effect (Negative, Positive and Neutral) and considered as sample size the number of measurements for each effect (Table S2). Due to the heterogeneity of our data, we used the log-transformed odds ratio (OR) as a measure of the effect size, since it is not affected by unequal sampling sizes and does not vary across sampling methods (Haddock et al., 1998). We estimated the log-transformed odds ratio through the escalc function of the package metaphor (Viechtbauer, 2010). A negative OR indicates that the evaluated effects of climate changes are probably random, while a positive OR indicates that the odds of the climate changes causing the evaluated effects are high. The precision of the OR is estimated by the 95% confidence interval (CI), where larger CIs indicates lower precision of the OR. Finally, we performed a chi-square test and generate correlation matrices by using the package corplot (Wei and Simko, 2017), to search for a relationship between the characters extracted from the studies.

## 3. Results and discussion

Most studies focused on species distributions (*N* = 86, 33.72%), followed by studies on thermal physiology (*N* = 74, 29.02%), reproductive biology (*N* = 34, 13.33%), behavior (*N* = 19, 7.45%) and genetics (*N* = 10, 3.92%) (Fig. 2). We analyzed 32 studies (12.54%) that approach general patterns and reviews in this subject. A total of 1918 species among 49 families were in overall addressed in the recorded studies (Table S3). The most representative family for each group was Scincidae (Lizards, 474 out of 1544 species addressed),

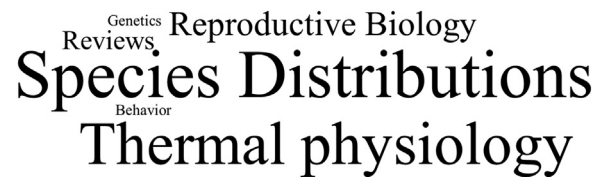


Fig. 2. Word clouds indicating most commonly analyzed subjects relating climate change and Lepidosauria. Subjects are listed with font size set to the number of times the category was addressed relative to others.

Colubridae (Snakes, 156 out of 362 species addressed) and Amphisbaenidae (Amphisbaenia, 6 out of 11 species addressed). The tuatara *Sphenodon punctatus* was also addressed. *Zootoca vivipara* was the most well documented species, being addressed by 20 articles, followed by *Sceloporus undulatus*, addressed by 12 articles. *Zootoca vivipara* is a widespread species that inhabits peat bogs and heathlands across northern Eurasia (Dupoué et al., 2017a), while *S. undulatus* is a North American widespread species, which has been used as a model system for understanding thermal physiology and its influences on population dynamics and range limits (Buckley et al., 2015).

### 3.1. Responses of Lepidosauria to current climate change

Taxonomic level was strongly associated with both main subject ( $\chi^2_{(20)} = 57.83$ ,  $p < 0.001$ ), and location of research ( $\chi^2_{(40)} = 75.33$ ,  $p < 0.001$ ), with species distribution (27.48% to the total chi-square score) and Australian realm (37.74% to the total chi-square score) accounting for most of the differences between expected and observed values (Fig. 3). The species distribution is the trend topic among the studies, since it is actually a result of all other topics addressed when we considered the concept of extinction risk, which is the risk of the mortality (and emigration) rate to be greater than the birth (and immigration) rate for a sufficiently long time that the population size reaches zero (Mace et al., 2008), so its relevance to the chi-square score is justified. Also, considering the restriction of the Tuatara's distribution to the Australian realm, it is logical that we found a great relevance of this realm to the chi-square score.

Most of the studies (*N* = 158) pointed to negative effects of climate change on Lepidosaurians; 31 pointed to positive effects, 39 were neutral and 27 did not evaluate this influence. Our meta-analysis demonstrated the strength of the climate change effects on Lepidosauria ( $I^2 = 0$ ,  $p < 0.0001$ ; Fig. 4), without heterogeneity presented ( $Q(df) = 0.2866$ ,  $p = 0.866$ ). We found high positive OR values and low 95% CIs for all three evaluated effects (Fig. 4). Also, the random effect model recovered a predictions' accuracy of  $97.99\% \pm 0.13$ . These results indicate that the current literature present robust and precise analyses that statistically corroborates the existence of both negative, positive and neutral effects of climate changes on Lepidosauria.

Our review highlights several biological characteristics of Lepidosaurians that may be directly influenced by changes in environmental conditions, and the state of the knowledge about the possible responses to this influence. We summarized the Lepidosaurians' biological characteristics that are directly or indirectly influenced by climate changes, and the possible responses raised by the studies (Table 1). Each of these characteristics is described below.

### 3.2. Species distributions

To track their climate niche, species can shift their distribution range, dispersing from cooler habitats when preferred temperatures (*T*<sub>pref</sub>) are high and from hotter habitats when *T*<sub>prefs</sub> are low (Bestion et al., 2015a). It means that climate change can have both positively and negatively effects for a particular species, by increasing or decreasing the availability of suitable thermal environments and thus expanding or retracting the species distributions (Alvarez et al., 2017;

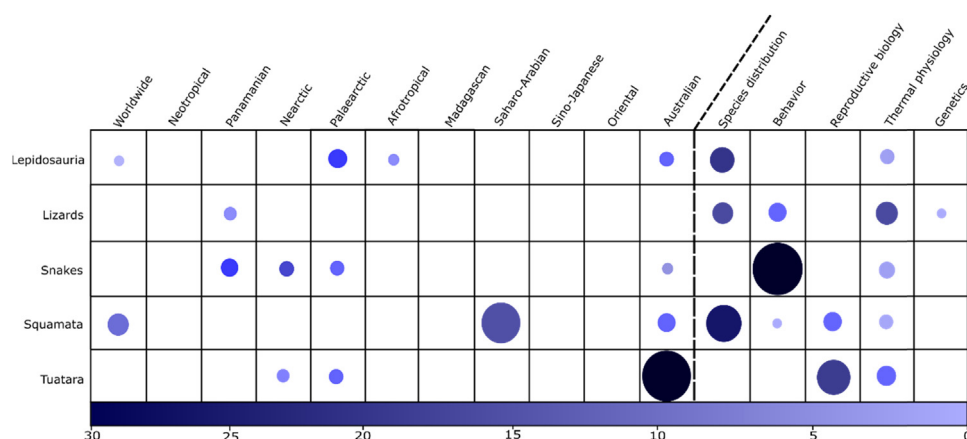


Fig. 3. Contribution (in %) of different taxonomic groups to the total Chi-square score obtained by relating groups, zoogeographical realms and subjects covered. The size of the circle and degree of color transparency is proportional to the amount of the cell contribution.

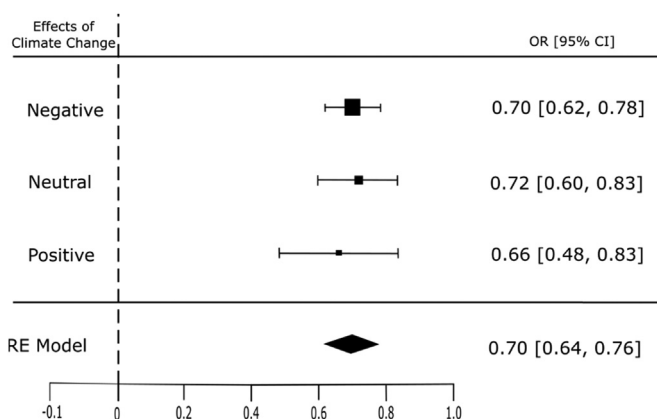


Fig. 4. Association between climate change and the vulnerability of Lepidosauria. RE model = Random effects; OR = Log Odds Ratio; CI = Confidence Interval. The x-axis represents the OR, or the meta-analysis' absolute statistics, varying from  $-0.1$  (low accuracy of the climate change effect) to  $1$  (high accuracy of climate change effect). Vertical dotted line represents the null effect. The size of the squares represents the size of the group effect in the analysis.

Bezeng et al., 2017; Yuan et al., 2018). For species with restricted distribution, this may be the threshold between survival and extinction (Bonino et al., 2014; Davis et al., 2015). Suitable habitats may shift across altitudinal, latitudinal and longitudinal gradients. Some species may need to migrate from lowlands to higher elevations (Barrows, 2011; Nasrabadi et al., 2017), others need to shift long distances to reach new suitable habitats, which success will depend on the species migration capacity (Araujo et al., 2006; Ofori et al., 2017). Marine snakes are also dispersing from beyond their typical distribution range, as a result of ocean warming due to climate change, by using ocean currents to reach relatively long-distance dispersal (Park et al., 2017). These climate-forced migrations, due to absence of suitable habitats on current species distribution, may lead some species to overlap their climate niche in the new occupied habitat, which will likely increase interspecific competition (Bombi et al., 2011a), which can be critical when such migrating are invasive species that are predicted to expand its distribution across the invaded country (Rodda et al., 2009).

Anthropogenic habitat transformation can affect distribution ranges and migration patterns, since anthropogenic landscapes can provide a fragmentation of the species habitat and function as a barrier to the species dispersion (Munguia-Vega et al., 2013; Gadsden et al., 2012; Ballesteros-Barrera et al., 2007). Species' biological characteristics can also influence their range shifts. TSD reptiles where males are produced

under higher temperatures, such as Tuatara, females become the rare sex as temperature rises, and if dispersal by females occurs, it may not facilitate successful reproduction driving to trends in male-male aggression when competing for females (Boyle et al., 2016). In these cases, dispersal was only observed in one instance to lead to notable range expansion (Boyle et al., 2016). The evolution of viviparity in most reptiles is associated with cold climates, and projections of climate change predict that under persistent warming, some viviparous may experience several range contractions followed by major extinction events within the next few decades, considering the evidence for irreversible parity mode (Pincheira-Donoso et al., 2013).

Paleoclimate models are a useful tool to estimate species or lineages responses to past climate change and to compare past, current and future predictions, seeking for patterns of changes in species distribution and establishing a framework to predict more accurate responses of species under current and future climate change scenario (e.g., Lawing and Polly, 2011; Sillero and Carretero, 2013; Barrows and Fischer, 2014; Martínez-Méndez et al., 2015; Yousefkhani et al., 2017). For current and future distributions, correlative models usually consider bioclimatic variables, such as mean annual temperature, seasonality and annual mean precipitation, as informative to predict future changes in suitable habitats for species (e.g., Houniet et al., 2009; Carvalho et al., 2010; Davis et al., 2015; Nasrabadi et al., 2017; Yousefkhani et al., 2017). Mechanistic models also include life history and ecophysiological traits, thermal tolerance, thermal preference, time of activity and operative temperature (e.g., Sinervo et al., 2010; Cabrelli et al., 2014; Ceia-Hasse et al., 2014; Bonino et al., 2015; Andrango et al., 2016; Kubisch et al., 2016). For lizards, this kind of model predicted local extinctions for species in 34 families worldwide by 2070, considering the hours of restriction in thermal refuges, which limit foraging and constraining costly metabolic functions (Sinervo et al., 2010). Mechanistic models work as a complement to correlative models for predict range dynamics of reptiles, since their performance improves when incorporating additional factors in comparison to correlative models (Buckley, 2010). Leaf litter, evapotranspiration and bioenergetics are some of these factors that must improve the performance of this kind of model (Whitfield et al., 2006; Buckley, 2008).

Species distribution models can also be used to determine the degree of species' vulnerability in different biomes and environments, and also verify the relationship between hotspots of climate change vulnerability and hotspots of threatened species richness, in order to supplement IUCN Red List assessments by highlighting species which may become highly threatened over time (Böhm et al., 2016). Protected areas may play an important role on the mitigation of the negative effects of climate change on reptile populations (Bombi et al., 2011b; Martínez-Freiría et al., 2013; Popescu et al., 2013; Bezeng et al., 2017;



**Table 1**  
Summary of potential effects of Climate Change on different parameters of the ecology/natural history and general biology from Lepidosauria.

Group affected	Main topical themes	Impact suffered	Observed responses	Possible tools to buffer effects	Source
Squamata	Genetics	low gene flow between populations	Vulnerability, local extinctions	–	Tolley et al. (2009), Clark et al. (2011), Dubey et al. (2013), Koumoundouros et al. (2013)
Squamata	Genetics	Telomere attrition	Change in age processes, population declines	–	Dupoué et al. (2017b)
Squamata	Reproductive Biology	"hot and dry" condition	Changes in Reproductive output, population declines	Physiological plasticity, acclimatization	Lelièvre et al. (2013), Pomarara et al. (2014), Jones et al. (2016), Wang et al. (2016), Westphal et al. (2016), Flesch et al. (2017)
Squamata	Reproductive Biology	colder condition	Changes in metabolism maintenance	–	Lelièvre et al. (2013), Flesch et al. (2017)
Rynchocephalia	Reproductive Biology	Male-biased sex ratio	Population declines	Translocation to cooler environments	Nelson et al. (2002), Mitchell et al. (2008), Mitchel et al. (2010), Grayson et al. (2014)
Squamata	Reproductive Biology	Female-biased sex ratio	Changes in population dynamics	Maternal nesting behavior, nesting phenology	Doody et al. (2006)
Squamata	Reproductive Biology	Availability of optimal nest sites	Changes in offspring and maternal fitness	Changes in nest-site selection	Huang and Pike (2011), Levy et al. (2015)
Squamata	Reproductive Biology	Hotter incubation	Changes in phenotypical traits and population dynamics	–	Massot et al. (2008), Amiel et al. (2012), Bell et al. (2013), Dayananda and Webb (2017), Carlo et al. (2017), Noble et al. (2017)
Squamata	Reproductive Biology	Changes in thermal performance	Decrease of hatching success and growth; changes in morphology traits	–	Bull and Burzacott (2002), Ijüngström et al. (2015), Prodon et al. (2017)
Squamata	Reproductive Biology	Incubation period	Embryonic mortality	mating with additional males	Olsson et al. (2011), Lu et al. (2013)
Squamata	Reproductive Biology	Rainfall	Decrease of neonates survival	mating with additional males	Marquis et al. (2008), Olsson et al. (2011)
Squamata	Reproductive Biology	Prey availability	Changes in reproductive event	–	Ujvari et al. (2011b)
Viviparous	Reproductive Biology	High cloud cover	Changes in maternal pregnancy success, population dynamics	–	Hare and Cree (2010)
Viviparous	Reproductive Biology	Exposure to different levels of hormones	Changes in dispersal ability and population dynamics	–	Meylan et al. (2012)
Snakes	Reproductive Biology	Increase of air temperature	Reduced above-ground activity and feeding	–	Moreno-Rueda et al. (2009), Rugiero et al. (2013), Capula et al. (2014)
Squamata	Species distribution	Changes in suitable habitats	Changes in species distribution	migration capacity, protected areas	Araujo et al. (2006), Barrows (2011), Bezeng et al. (2017), Caten et al. (2017), Minoli and Avila (2017), Nasrabadi et al. (2017), Nori et al. (2017), Ofori et al. (2017)
Squamata	Species distribution	climate-forced migrations	Interspecific competition	–	Rodda et al. (2009)
Viviparous	Species distribution	Range contractions	Extinction events	–	Pincheira-Donoso et al. (2013)
Rynchocephalia	Species distribution	Low dispersal capacity	Local extinctions	Assisted colonization	Fordham et al. (2012), Miller et al. (2012), Jarvie et al. (2014)
Squamata	Behavior	Stressful abiotic conditions	Increase of competition	–	Buckley (2013)
Squamata	Behavior	Changes in gut microbiota	Dysbioses, host survival	–	Bestion et al. (2017)
Squamata	Behavior	Increase temperature and humidity	Increase of predation	–	Cox et al. (2013), DeGregorio et al. (2015), George et al. (2015)
Squamata	Behavior	Local scale perturbations	Changes in resource selection by predators	–	George et al. (2017), Rugiero et al. (2012)
Squamata	Behavior	Changes on seasonal migration of preys	Unability to track preys	–	Ujvari et al. (2011a)
Squamata	Thermal physiology	Behavioral thermoregulation	Changes in physiological traits	–	Keamey et al. (2009), Goller et al. (2014), Llewellyn et al. (2016), Artacho et al. (2017)
Squamata	Thermal physiology	Incubation temperatures	Changes in embryonic thermal physiology and morphology	–	Andrew and Schwarzkopf (2012), Amiel et al. (2016), Gilbert and Lattanzio (2016), Simoniello et al. (2016)
Squamata	Thermal physiology	Local heat waves	Changes in sexual chemical signals, immune functions	–	Martin and López (2013), Stahlschmidt et al. (2017)
Squamata	Thermal physiology	Increase operative temperature	Increase of energy expenditure and changes on thermoregulatory strategy	Shade availability, use of refuges	Weatherhead et al. (2012), Valenzuela-Ceballos et al. (2015), Basson et al. (2016), Medina et al. (2016), Levy et al. (2017)
Squamata	Thermal physiology	Temperature and precipitation variation	Changes in thermal physiology, Natural Selection	Physiological plasticity, acclimatization	Clusella-Trullas et al. (2011), Brischoux et al. (2015), Buckley et al. (2015), Ferri-Yáñez and Araújo (2015), Ortega et al. (2016b), Putman and Clark (2017), Theisinger et al. (2017)

Caten et al., 2017; Minoli and Avila, 2017; Nori et al., 2017). Species with predicted decreases in their amount of suitable habitats may use the protected areas as ecological corridors, allowing their dispersal (Caten et al., 2017). However, some species may present both good coverage and connectivity within the existing protected network, but still suffer loss of genetic variability as an effect of climate change, which demonstrate that the management of protected areas must to consider all the processes that threaten the species to improve a successful prospective conservation (Rödder and Schulte, 2010).

Human-induced translocation of most sensible populations to more thermal suitable habitats, or assisted colonization, can be a strategy to buffer the effects of climate change in species with restricted distributions and low dispersion capacity (Fordham et al., 2012), and is commonly applied in tuatara populations (Miller et al., 2012; Jarvie et al., 2014). In that case, it is important to analyze several outcomes besides thermal suitability for the focal species, such as the possibility that the species will colonize the introduction sites naturally, the performance of translocated individuals in their new environment and the consequences of the introduction in local biodiversity (Besson and Cree, 2010; Rout et al., 2013). Reptiles' distribution shifts due to global warming may also be a subject of concern for human populations, since future projections indicate possible displacements of venomous snakes to human populated areas increasing rate of contact, which in turn, may increase the snakebite envenoming in light of climate change (Nori et al., 2014).

### 3.3. Thermal physiology

A premier principle in ecological physiology is that population exposed to environmental change may crash when most individuals deteriorate, and that individuals decline when they reach a physiological state that prevents them for maintaining homeostasis (Naya et al., 2011). The most addressed subject among ecophysiological studies on climate change and Lepidosauria is if environmental temperatures will exceed the species' physiological tolerance, and what possible responses can species develop. The *trade-off hypothesis* predicts that organisms with inherent thermal tolerance will present lower plasticity, which could mean that species with highest thermal tolerance may be most vulnerable to changes in environmental temperatures, if these changes exceed the limits of tolerance (Gunderson and Stillman, 2015). This counterintuitive prediction was tested in several studies regarding thermoregulatory capacity, thermal performance and behavioral plasticity, being supported, at least partially, by some (e.g., Aubret and Shine, 2010; Brusch et al., 2015; Kirchhoff et al., 2017), and rejected by others (e.g., Logan et al., 2013; Aguado and Braña, 2014; Li et al., 2017).

Behavioral thermoregulation may change along gradients of climate conditions and produce counter-gradient variation in physiological traits (Llewelyn et al., 2017), but which factors influence its optimization and its degree of evolutionary lability remains uncertain (Kearney et al., 2009; Goller et al., 2014; Llewelyn et al., 2016; Artacho et al., 2017). Forest cover is one of these factors, since increasing forest canopy gradually cools the microclimates, and hence decreasing body temperature (Huang et al., 2014a), while the loss of shaded microhabitat increases the impact of climate change (Kearney, 2013; Ackley et al., 2015; Grimm-Seyfarth et al., 2017). Wind speed and water flux and balance are also important, since they affect the costs and benefits of thermoregulation by reducing the daily activity, complicate the hunting of prey or increase desiccation (Belasen et al., 2016; Ortega et al., 2016a; Pintor et al., 2016; Dupoué et al., 2017a).

Measurements on precision of thermoregulation are usually addressed to evaluate the thermal quality of habitat, thermoregulation accuracy and effectiveness of thermoregulation (Hertz et al., 1993). In a challenging environment, basking behavior accounting for most of energy consumed, rather than locomotion, since animals exerted more effort to actively thermoregulates, limiting access to resources

distributed throughout space (Basson et al., 2016). Energy expenditure followed spatial patterns in thermal opportunity, and reptiles should spend more energy under climate change by maintaining higher body temperatures and remaining active longer (Levy et al., 2017). Species that present greater abundance in environments thermally less favorable may prioritize habitats with adequate refuges from adverse environmental conditions and predators or with available prey or food rather than to maintain constant thermoregulation (Valenzuela-Ceballos et al., 2015; Medina et al., 2016). Also, viviparous species may experience stronger selective pressures for females that basking at higher temperatures, due to the need of restore energy reserves after parturition, and this condition may put these species at a higher risk of extinction due to climate change (Bleu et al., 2013; Paranjpe et al., 2013; López-Alcaide et al., 2017; Telemeco et al., 2017; Wang et al., 2017).

Environmental temperatures are better predictors of life-history variation than body temperatures (Meiri et al., 2013), although higher body temperatures in thermally constrained environments may allow for faster life cycles (Artacho et al., 2017). Some fitness-influencing components of performance are more closely related to temperature variation and precipitation than to mean thermal conditions, which may indicate that these environmental traits have had a strong influence on the evolution of ectotherm performance (Clusella-Trullas et al., 2011). The relationship between thermal environment and body temperature is thus what ultimately influences the organismal physiology (Brischoux et al., 2015; Ferri-Yáñez and Araújo, 2015) although activity rates may be more sensitive to temperature than physiological traits for some species (Gunderson and Leal, 2015, 2016).

Some terrestrial reptiles may experience strong natural selection in warmer microhabitats, which could drive to shifts in thermoregulatory strategies associated to shifts in thermal physiology (Logan et al., 2014). However, species subjected to similar environmental constraints can diverge in thermoregulatory strategy due to coadaptation between traits (Angilletta et al., 2006), and thus may exhibit divergent energy budgets, foraging modes and habitat use, besides to be associated with different demographic characteristics and sensitivity to climate conditions (Lelièvre et al., 2013). Failure to thermoregulate can expose animals to temperatures that select for a greater critical thermal limit, greater performance and warmer thermal preferences (Buckley et al., 2015; Ortega et al., 2016b). Behaviorally avoiding exposed and sunny microhabitats during the hottest periods of the day may buffer these selective pressures imposed by hotter microhabitats (Sinervo et al., 2010; Gilbert and Miles, 2017). Thus, habitat features, such as shade availability and refugia sites, are essential to allow this behavior (Kearney et al., 2009). In addition, changes in thermal tolerance of tropical species can occurs relatively rapidly, along few generations, which may indicate that thermal physiology in these species is more labile than is usually inferred (Leal and Gunderson, 2012).

The thermal quality of the environment should influence the reptiles' thermoregulatory strategy (Huey and Slatkin, 1976; Scheffers et al., 2014), since it may affect the time and energy expended to maintain optimal body temperatures (Weatherhead et al., 2012). Thermal performance curves constitute useful tools to measure out the tolerance zone and optimal body temperature for reptiles, and thus to evaluate if thermal physiology is subject to natural selection (Clusella-Trullas and Chown, 2014; Sinclair et al., 2016). Speed-related performance traits, such as sprint speed and endurance, are highly temperature-dependent whereas force-related traits, such as bite, hand and tail force, are less dependent on temperature (Segall et al., 2013). Thus, most of studies regarding thermal performance and climate changes focused on speed-related traits (Logan et al., 2014; Kubisch et al., 2015; Yuan et al., 2016; Gilbert and Miles, 2017).

Latitudinal and altitudinal gradients are also relevant for species' thermal biology. Temperate zone species usually bask and are restricted to open habitats with high and heterogeneous environmental operative temperatures, while tropical and subtropical species present a more

diverse thermoregulatory behavior, since its landscapes provide sufficient within-site thermal heterogeneity for marked physiological trait specialization (Huey et al., 2009; Piantoni et al., 2015; Muñoz et al., 2016). At least in short term, temperate species are predicted to benefit themselves from increases in temperature, while activity of tropical species is predicted to decrease (Huey et al., 2009; Caldwell et al., 2015). Also, mountain cold-specialists are predicted to be the most vulnerable group among reptiles, due to their thermal reaction norms, in which as long as temperature decreases from the optimal, its survival decreases slowly, but then rapidly when temperature surpasses the optimal (Huey et al., 2012; Ortega et al., 2016c, 2016d). However, these animals may be better able to handle hypoxic conditions that may cause a dramatically reduction in temperature set point of reptiles (DuBois et al., 2017).

### 3.4. Reproductive biology

The species' vulnerability depends on the sensitivity of every stage of the life cycle (Levy et al., 2016). Embryonic thermal physiology and ontogeny are adapted to large-scale environmental patterns, and variations on climate conditions may lead to a large impact of climate change on these traits (Andrew and Schwarzkopf, 2012; Gilbert and Lattanzio, 2016). Climate variation also has been found to affect the reproductive timing, with pairing tending to start earlier and persisting for a longer time (Bull and Burzacott, 2002; Ljungström et al., 2015; Prodon et al., 2017), and performance, affecting hatchling success, morphological traits and growth (Monasterio et al., 2013).

Some temperate species may be benefited by warmer nights, such as *Uta stansburiana*, which present as positive fitness effects the increase of its development rate and advance of reproductive phenology (Clarke and Zani, 2012). However, hotter incubation temperatures usually decrease incubation period across reptiles, and can influence several phenotypical traits, such as morphology, development, performance, behavior, physiology and survival, being the last three the most affected traits in Squamata (Noble et al., 2017, e.g., Carlo et al., 2017).

Contemporary climate change has also the potential to alter the location and availability of 'optimal' nest sites, which may influence both offspring and maternal fitness (Huang and Pike, 2011). With the predicted changes in environmental temperatures, females should construct shadier nests, where temperatures will not increase sufficiently to threaten embryos or where mothers should already nest in full shade (Levy et al., 2015). In spite of this need, some species may present low plasticity in maternal nest-site selection, such as communal nesting species, which may increase the impacts of climate change in their hatchling survival if they occupy thermally challenging environments (Dayananda et al., 2016).

Successful embryonic development is usually linked to incubation period, which is likely to be comprised by available thermal conditions for several species, demonstrating the negative effects of high temperatures (Lu et al., 2013; Monasterio et al., 2013). Exposure to stressful but non-lethal temperatures during the development can influence the hatchlings brains' morphology, volume and the absolute size at hatching, suggesting that it had a tissue-specific effect on the brain (Amiel et al., 2016; Simoniello et al., 2016). Hotter nests may also influence locomotor performance and learn ability of hatchlings, which may consequently influence their dispersal and survival rates (e.g., Amiel et al., 2012; Bell et al., 2013; Dayananda and Webb, 2017).

An increase in interannual temperature variation could lead to significant fluctuation in cohort sex ratios, which may have important effects on population dynamics if leading to adult sex ratio bias (Wapstra et al., 2009; Mitchel et al., 2010). Demographic stochasticity, differential survival of each sex and environmental conditions are some of the causes of biased sex ratios, which is a recognized problem for species conservation (Grayson et al., 2014). Some reptiles, such as tuataras, have temperature-dependent sex determination (TSD), where incubation temperature during a specific period of embryonic

development determines sex (Bull, 1980). Some populations of tuatara are already facing an increase in male bias, which may lead these populations to become extinct, considering the higher male-male competition and the production of fewer offspring (Grayson et al., 2014). Also, future predictions demonstrate that without adaptation, climate change will produce fast-developing all-male clutches, increasing the extinction risk of these populations (Mitchell et al., 2008). Warmer weather during nest construction may result in shorter nest seasons, and the deposition of eggs earlier in the season may result in higher average temperature of nests, which may justify the populations' male bias condition (Nelson et al., 2004). Also, the absence of any adjustment of nesting behavior may lead to reduced recruitment as a result of lethal temperature in nests. Neither modifying nesting behavior nor adaptive response of pivotal temperature can modify sex ratios fast enough for tuatara, so a useful tool to buffer the effects of climate change on its phenology is the translocation to cooler environments, rather than periodic intervention, which may be more costly (Mitchel et al., 2010).

Besides tuatara, others Lepidosaurians also present environmental sex determination, and for those evidences suggest that climatic differences would be compensated by maternal nesting behavior and nesting phenology (Doody et al., 2006). Some species have already adjusted both nest depth and seasonal timing of oviposition in response to rising ambient temperatures, although have been unable to compensate entirely for climate change, resulting in mean incubation temperatures higher than the thermal threshold at which incubation temperature directly affects offspring sex (Telemecco et al., 2009). Some viviparous lizards present temperature dependent gestation length, and population's specific effects of temperature (Cunningham et al., 2017). In contrast to tuataras, the most affected lizard populations by warmer environments will present a female-skewed sex ratio, which may not have a negative effect on the population growth rates, since it is generally determined by the number of females particularly in species where males may mate with multiple females (Cunningham et al., 2017).

Rainfall regime can also be relevant for reproductive performance, since some species experiencing higher rainfall rate during gestation produced smaller neonates with greater survival, while females experiencing heavier rainfall produced fewer but longer neonates (Marquis et al., 2008). Low precipitation and drought increases can also affect species survival, and a drier and hotter environment can affect negatively the gestation period and reproductive output of females and the offspring sex ratio (Wang et al., 2016; Westphal et al., 2016). A strategy used by some species in consequence of warmer environments is the mating with additional males, which enhance the viability of a female's offspring via sperm competition and increase the first-year survival of hatchlings (Olsson et al., 2011). Changes in the reproductive event may also occurs by indirect effects of climate change, such as prey availability, where under food deprivation some species may respond by reproducing at body sizes far below the usual (Ujvari et al., 2011a).

In viviparous species, thermal conditions during different stages of gestation may affect different aspects of reproduction, such as embryo viability, gestation length and offspring phenotypes (Lourdais et al., 2004). When exposed to longer basking opportunities per day, some species can give birth earlier to smaller offspring that grow faster in the first few weeks of life, which demonstrates a possible resilience by the species in a warmer environment (Dubey and Shine, 2011). High cloud cover may lead to lower and slower growing, and thus smaller female offspring, demonstrating its potential long-term influence on population dynamics (Hare and Cree, 2010). Females exposed to thermal stressors during reproduction may alter the phenotypes by manipulation of hormones to the embryos (Meylan et al., 2012). Variation in exposure to hormones during development influences both the propensity to disperse and population dynamics, by affecting either recruitment to the population or subsequent life-history characteristics of the offspring (Meylan et al., 2012).

### 3.5. Behavior

Although more difficult to predict, climate-mediated changes to intra and interspecific relationships could have profound ecological effects (DeGregorio et al., 2015). The degree of species interactions and how they may be altered by climate change can be estimated by species traits, and in response to climate change it can accentuate abundance and distribution shifts (Buckley, 2013). Such estimates are still surrounded by uncertainties and demand cautious interpretation of the observed patterns (Cox et al., 2013).

Buckley (2013) focused on competition of Caribbean *Anolis* to evaluate the influence of climate change on species interactions. She observed that competition is more intense in stressful abiotic conditions, primarily at the range edge contact zone. Thus, it may accentuate the species' abundance and distribution shifts, since the forest-dweller, *Anolis gundlachi*, may present a competitive displacement due to the movement of the open and edge habitat-dweller, *Anolis cristatellus*, to its preferred microhabitat (Buckley, 2013).

Rabosky et al. (2012), in turn, focused on access climate change influences on social aggregation of *Xantusia vigilis*, a nocturnal lizard from the western Mojave Desert. They observed that social aggregation may increase thermal buffering and reduce eventually metabolic costs caused by climate change (Rabosky et al., 2012).

Bestion et al. (2017) evaluate the symbiosis between animal hosts and the bacterial community inhabiting their guts. This relationship is shaped by hosts providing immunity and metabolism, and gut microbiota providing the improvement of essential functions for hosts, such as digestion (Bestion et al., 2017). Changes in temperature may lead to changes in gut microbiota, which in turn may lead to potential dysbiosis, with possible negative consequences for host survival (Bestion et al., 2017).

Despite the studies mentioned above, most of studies regarding species interactions of Lepidosaurians and climate change focus on predation. Increased temperatures and relative humidity allow nest predators to become more active earlier in the year, which may lead to an increase of nest predation in warmer seasons (Cox et al., 2013; DeGregorio et al., 2015; George et al., 2015). Heterogeneity of canopy cover and local scale perturbations also influences the resource selection by predators (George et al., 2017; Rugiero et al., 2012). Changes in seasonal migration of preys due to climate changes may lead inflexible predators, or such species that track seasonally migrating preys by responding to habitat attributes rather than to proximate cues that signal the preys' presence, to be indirectly more vulnerable to global warming (Ujvari et al., 2011b). Also, thermophilic species may be favored by the increase in mean temperatures, as it may enhance their foraging performances and hence their feeding frequencies (Capula et al., 2015).

#### 3.5.1. Metabolism and energetics

Phylogenetic trends, metabolism and energetics also provide useful physiological explanations for the rates of current and future climate-forced extinctions (Medina et al., 2012; Huang et al., 2013; Logan et al., 2015; Dupoué et al., 2017c). Given the importance of temperature for biochemical reactions, the physiological impacts of climate and temperature are likely manifest in most physiological functions. For example, femoral secretions, which are key sexual chemical signals for intersexual interactions, are negatively impacted by increased temperature in the mountain lizard, *Iberolacerta cyreni* (Martín and López, 2013). In addition, innate immune function has been shown to be reduced by local heat waves in the corn snake *Pantherophis guttatus* (Stahlschmidt et al., 2017).

Species may present physiological compensation, plasticity and acclimatization as a supplementary mechanism to compensate thermal challenges (Putman and Clark, 2017; Theisinger et al., 2017). Stressful environmental temperatures may increase the energetic costs of metabolism maintenance during dormancy or nocturnal inactivity or reduce the quality of low-temperature thermoregulatory refugia (Lelièvre

et al., 2013; Flesch et al., 2017). The adverse climatic conditions may lead some species to a decrease of lower heat tolerance, possible due to the increase of heat shock proteins (HSPs), which apparently have this effect in other organisms when are upregulated by high temperatures (Dayananda et al., 2017). Also, it may reduce the secretions of corticosterone in lizards, downregulating the individuals' activity levels to avoid water loss (Dupoué et al., 2018).

For some lizards, shifts in morphotypes and body size are related to thermoregulation capacities (Lepetz et al., 2009; Kubisch et al., 2012; Huang et al., 2014b). Larger lizards are more likely to survive longer regardless of winter temperature, and longer growing seasons may offset losses by allowing additional growth and energy storage (Zani, 2008). Warmer temperatures could also cause faster body growth, which may be associated to larger clutch sizes and total reproductive output (Chamaillé-Jammes et al., 2006), but also to an earlier reproductive onset and an increased voltinism, leading to a highly accelerated life cycle, but also to a decrease in adult survival for some species (Bestion et al., 2015b).

#### 3.5.2. Population dynamics

Changes on seasonal activities are the most well documented organisms' response to climate change, since it is a key trait that influences individuals' fitness and population dynamics (Massot et al., 2017). Climate variables are local and temporally dynamic and may cause important effects on both individual and life history processes of ectotherms, leading to spatiotemporal changes in their true abundance (Cowles and Bogert, 1944; Dunham et al., 1989).

For snakes, above ground activity, feeding period and hibernation are important aspects for their population dynamics (Rugiero et al., 2013), and may vary as a compensatory response to global warming. Increasing mean air temperatures can cause an earlier onset of above-ground activity and feeding, and delayed hibernation, besides reduced the intensity of snake above-ground activity during the hottest and driest period of the year (Moreno-Rueda et al., 2009; Rugiero et al., 2013; Capula et al., 2014). These strategies may buffer the effects of increased temperature in species whose predictions are that temperature variation does not negatively affect their population dynamics, despite the species exposure to warmer environments (e.g., *Hierophis viridiflavus*, Lelièvre et al., 2013).

### 3.6. Genetics

Understanding patterns of gene flow is crucial for the design of effective conservation strategies for threatened reptiles (Koumoundouros et al., 2013). Phenotypic divergence is aligned with genomic divergence in response to changes in climate (Prates et al., 2016), due to the connection between long-term evolutionary adaptation to an environmental selective agent and short-term stress response in individual organisms (Rodríguez et al., 2017). A functional genomic network for thermoregulation and thermal adaptation may be regulated by similar evolutionary conserved pathways among several vertebrate lineages, which validates a comparative approach to understanding thermal adaptation (Rodríguez et al., 2017). Also, telomere length is a promising biomarker to raise the alarm regarding early population decline, since telomere attrition accelerates age processes after a recurrent exposure to environmental stressors (Dupoué et al., 2017b).

Species that are restricted to habitat fragments, especially if population subdivisions persisted over evolutionary time and have generated genetic discontinuity across the species' range, should present higher vulnerability to climate change if the sites that contain most of the species' genetic variation would be also among the most affected areas (Clark et al., 2011; Dubey et al., 2013; Koumoundouros et al., 2013). When connectivity between suitable patches is reduced and estimates are of low gene flow between populations, the implication is that distance between fragments will increase, which can lead to two consequences: vicariance through fragmentation, which demands an



increase in population size and ecological requirements, or a possible local extinction if these factors decreases rather than increases, which in a scenario of climate change is more likely to occur (Tolley et al., 2009). Thus, specialist species are likely to be constrained in their evolutionary responses to future climate changes (Afonso Silva et al., 2017).

Parallel microevolution within separate species can demonstrate natural selection to climate variation, which is important to determine if natural populations can adapt to climate change (Thorpe et al., 2015). Some species, such as anoles, also have the capacity for rapid adaptation, which may neutralize the possible negative effects of climate change (Thorpe et al., 2015). Also, peripheral and long-isolated lineages may differ physiologically from larger centrally located lineages and shelter genotypes that may confer resilience to global warming (Moritz et al., 2012).

#### 4. Conclusions

1. The most approached subject among the studies on climate change influence in Lepidosauria has been species distributions, since it is actually a result of all other topics addressed when we considered the concept of extinction risk, which is the risk of the mortality (and emigration) rate to be greater than the birth (and immigration) rate for a sufficiently long time that the population size reaches zero;
2. Most of the studies pointed to negative effects of climate change on Lepidosaurians, with no effects of heterogeneity, which highlights their vulnerability to temperature variation;
3. An integrative approach including most of the characteristics presented here (e.g. genetics, population dynamics, species distributions, behavior and thermal physiology), and also bioclimatic and environmental variables, may lead to consistent and truly effective strategies for species conservation, aiming to buffer the climate change effects on this group of reptiles.

#### Acknowledgements

We are grateful to R. T. Figueroa, who provided helpful and enlightenment suggestions on the former design of the study, and to B. Cosendey, O. Barbosa, M. Kajin and F. Scarano for their review in this paper. Universidade do Estado do Rio de Janeiro (UERJ) and Programa de Pós-Graduação em Ecologia e Evolução provided many logistic support.

#### Funding sources

LMDV benefitted from grants of the Coordenação de Aperfeiçoamento de Pessoal de Nível Superior (CAPES, process Nos. 88881.188452/2018-01 and 1684534). CFDR benefitted from grants of the Conselho Nacional de Desenvolvimento Científico e Tecnológico (CNPq, process Nos. 302974/2015-6 and 424473/2016-0) and from Fundação Carlos Chagas Filho de Amparo à Pesquisa do Estado do Rio de Janeiro (FAPERJ) through “Cientistas do Nosso Estado” Program (process No. E-26/202.920.2015) and FAPERJ/Biota Program (process No. E-26/010.001639/2014).

#### Appendix A. Supplementary material

Supplementary data associated with this article can be found in the online version at [doi:10.1016/j.jtherbio.2018.11.005](https://doi.org/10.1016/j.jtherbio.2018.11.005).

#### References

Ackley, J.W., Angilletta Jr., M.J., DeNardo, D., Sullivan, B., Wu, J., 2015. Urban heat island mitigation strategies and lizard thermal ecology: landscaping can quadruple potential activity time in an arid city. *Urban Ecosyst.* <https://doi.org/10.1007/s11252-015-0460-x>.

Afonso Silva, A.C., Bragg, J.G., Potter, S., Fernandes, C., Coelho, M.M., Moritz, C., 2017. Tropical specialist vs. climate generalist: diversification and demographic history of sister species of *Carlia* skinks from northwestern Australia. *Mol. Ecol.* 26, 4045–4058. <https://doi.org/10.1111/mec.14185>.

Aguado, S., Braña, F., 2014. Thermoregulation in a cold-adapted species (Cyren's Rock Lizard, *Iberolacerta cyreni*): influence of thermal environment and associated costs. *Can. J. Zool.* 92, 955–964. <https://doi.org/10.1139/cjz-2014-0096>.

Alvarez, G., Salas, E.A.L., Harings, N.M., Boykin, K.G., 2017. Projections of future suitable bioclimatic conditions of parthenogenetic whiptails. *Climate* 5, 1–21. <https://doi.org/10.3390/cli5020034>.

Amiel, J.J., Bao, S., Shine, R., 2012. Hotter nests produce smarter young lizards. *Biol. Lett.* 8, 372–374. <https://doi.org/10.1098/rsbl.2011.1161>.

Amiel, J.J., Bao, S., Shine, R., 2016. The effects of incubation temperature on the development of the cortical forebrain lizard. *Anim. Cogn.* <https://doi.org/10.1007/s10071-016-0993-2>.

Andrango, M.B., Sette, C., Torres-Carvajal, O., 2016. Short-term predicted extinction of Andean populations of the lizard *Stenocercus guentheri* (Iguanidae: tropidurinae). *J. Therm. Biol.* 62, 30–36. <https://doi.org/10.1016/j.jtherbio.2016.09.012>.

Angilletta Jr., M.J., Bennett, A.F., Guderley, H., Navas, C.A., Seebacher, F., Wilson, R.S., 2006. Coadaptation: a unifying principle in evolutionary thermal biology. *Physiol. Biochem. Zool.* 79, 282–294.

Andrew, R.M., Schwarzkopf, L., 2012. Thermal performance of squamate embryos with respect to climate, adult life history, and phylogeny. *Biol. J. Linn. Soc.* 106 (4), 851–864. <https://doi.org/10.1111/j.1095-8312.2012.01901.x>.

Araujo, M.B., Thuiller, W., Pearson, R.G., 2006. Climate warming and the decline of amphibians and reptiles in Europe. *J. Biogeogr.* 33, 1712–1728.

Araujo, M.B., Nogués-Bravo, D., Diniz-Filho, J.A.F., Haywood, A.M., Valdes, P.J., Rahbek, C., 2008. Quaternary climate changes explain diversity among reptiles and amphibians. *Ecography*. <https://doi.org/10.1111/j.2007.0906-7590.05318.x>.

Artacho, P., Saravia, J., Perret, S., Bartheld, J.L., Le Galliard, J.F., 2017. Geographic variation and acclimation effects on thermoregulation behavior in the widespread lizard *Liolaemus pictus*. *J. Therm. Biol.* <https://doi.org/10.1016/j.jtherbio.2016.11.001>.

Aubret, F., Shine, R., 2010. Thermal plasticity in young snakes: how will climate change affect the thermoregulatory tactics of ectotherms? *J. Exp. Biol.* 213, 242–248. <https://doi.org/10.1242/jeb.035931>.

Ballesteros-Barrera, C., Martínez-Meyer, E., Gadsden, H., 2007. Effects of land-cover transformation and climate change on the distribution of two microendemic lizards, Genus *Uma*, of Northern Mexico. *J. Herpetol.* 41, 733–740.

Basson, C.H., Levy, O., Angilletta Jr., M.J., Clusella-Trullas, S., 2016. Lizards paid a greater opportunity cost to thermoregulate in a less heterogeneous environment. *Funct. Ecol.* <https://doi.org/10.1111/1365-2435.12795>.

Barrows, C.W., 2011. Sensitivity to climate change for two reptiles at the Mojave Sonoran Desert interface. *J. Arid Environ.* 75, 629e635. <https://doi.org/10.1016/j.jaridenv.2011.01.018>.

Barrows, C.W., Fischer, M., 2014. Past, present and future distributions of a local assemblage of congeneric lizards in southern California. *Biol. Conserv.* 180, 97–107. <https://doi.org/10.1016/j.biocon.2014.09.042>.

Belasen, A., Brock, K., Li, B., Chremou, D., Valakos, E., Pafilis, P., Sinervo, B., Foufopoulos, J., 2016. Fine with heat, problems with water: microclimate alters water loss in a thermally adapted insular lizard. *Oikos* 126, 447–457. <https://doi.org/10.1111/oik.03712>.

Bell, K., Blomberg, S., Schwarzkopf, L., 2013. Detrimental influence on performance of high temperature incubation in a tropical reptile: is cooler better in the tropics? *Oecologia* 171, 83–91. <https://doi.org/10.1007/s00442-012-2409-6>.

Bellard, C., Bertelsmeier, C., Leadley, P., Thuiller, W., Courchamp, F., 2012. Impacts of climate change on the future of biodiversity. *Ecol. Lett.* 15, 365–377. <https://doi.org/10.1111/j.1461-0248.2011.01736.x>.

Besson, A.A., Cree, A., 2010. Integrating physiology into conservation: an approach to help guide translocations of a rare reptile in a warming environment. *Anim. Conserv.* 14, 28–37. <https://doi.org/10.1111/j.1469-1795.2010.00386.x>.

Bestion, E., Clobert, J., Cote, J., 2015a. Dispersal response to climate change: scaling down to intraspecific variation. *Ecol. Lett.* 18 (11), 1226–1233. <https://doi.org/10.1111/ele.12502>.

Bestion, E., Teyssier, A., Richard, M., Clobert, J., Cote, J., 2015b. Live fast, die young: experimental evidence of population extinction risk due to climate change. *PLoS Biol.* 13, e1002281. <https://doi.org/10.1371/journal.pbio.1002281>.

Bestion, E., Jacob, S., Zinger, L., Di Gesu, L., Richard, M., White, J., Cote, J., 2017. Climate warming reduces gut microbiota diversity in a vertebrate ectotherm. *Nat. Ecol. Evol.* 1. <https://doi.org/10.1038/s41559-017-0161>.

Bezeng, S.B., Tesfamichael, S.G., Dayananda, B., 2017. Predicting the effect of climate change on a range-restricted lizard in southeastern Australia. *Curr. Zool.* 1–7. <https://doi.org/10.1093/cz/zox021>.

Bleu, J., Le Galliard, J.F., Fitze, P.S., Meylan, S., Clobert, J., Massot, M., 2013. Reproductive allocation strategies: a long-term study on proximate factors and temporal adjustments in a viviparous lizard. *Oecologia* 171, 141–151.

Böhm, M., Cook, D., Ma, H., Davidson, A.D., García, A., Tapley, B., Pearce-Kelly, P., Carr, J., 2016. Hot and bothered: using trait-based approaches to assess climate change vulnerability in reptiles. *Biol. Conserv.* 204, 32–41. <https://doi.org/10.1016/j.biocon.2016.06.002>.

Bombi, P., Akani, G.C., Eber, N., Luiselli, L., 2011a. Potential effects of climate change on high- and lowabundance populations of the Gaboon viper (*Bitis gabonica*) and the nose-horned viper (*B. nasicornis*) in southern Nigeria. *Herpetol. J.* 21, 59–64.

Bombi, P., Capula, M., D'Amen, M., Luiselli, L., 2011b. Climate change threatens the survival of highly endangered Sardinian populations of the snake *Hemorrhois hippocrepis*. *Anim. Biol.* 61, 239–248. <https://doi.org/10.1163/157075511X584191>.

- Bonino, M.F., Azócar, D.L.M., Schulte II, J.A., Cruz, F.B., 2014. Climate change and lizards: changing species' geographic ranges in Patagonia. *Reg. Environ. Change*. <https://doi.org/10.1007/s10113-014-0693-x>.
- Bonino, M.F., Azócar, D.L.M., Schulte II, J.A., Abdala, C.S., Cruz, F.B., 2015. Thermal sensitivity of cold climate lizards and the importance of distributional ranges. *Zoology* 118, 281–290. <https://doi.org/10.1016/j.zool.2015.03.001>.
- Borenstein, M., Hedges, L.V., Higgins, J.P., Rothstein, H.R., 2011. *Introduction to Meta-Analysis*. John Wiley & Sons, United Kingdom.
- Boyle, M., Schwanz, L., Hone, J., Georges, A., 2016. Dispersal and climate warming determine range shift in model reptile populations. *Ecol. Model.* 328, 34–43. <https://doi.org/10.1016/j.ecolmodel.2016.02.011>.
- Brischoux, F., Dupoué, A., Lourdais, O., Angelier, F., 2015. Effects of mild wintering conditions on body mass and corticosterone levels in a temperate reptiles, the asp viper (*Vipera aspis*). *Comp. Biochem. Physiol. A* 192, 52–56. <https://doi.org/10.1016/j.cbpa.2015.11.015>.
- Brusch IV, G.A., Taylor, E.N., Whitfield, S.M., 2015. Turn up the heat: thermal tolerances of lizards at La Selva, Costa Rica. *Oecologia*. <https://doi.org/10.1007/s00442-015-3467-3>.
- Buckley, L.B., 2008. Linking traits to energetics and population dynamics to predict lizard ranges in changing environments. *Am. Nat.* 171 (1), E1–E19. <https://doi.org/10.1086/523949>.
- Buckley, L.B., 2010. The range implications of lizard traits in changing environments. *Glob. Ecol. Biogeogr.* 19, 452–464. <https://doi.org/10.1111/j.1466-8238.2010.00538.x>.
- Buckley, L.B., 2013. Get real: putting models of climate change ad species interactions in practice. *Ann. N. Y. Acad. Sci.* <https://doi.org/10.1111/nyas.12175>.
- Buckley, L.B., Ehrenberger, J.C., Angilletta Jr, M.J., 2015. Thermoregulatory behaviour limits local adaptation of thermal niches and confers sensitivity to climate change. *Funct. Ecol.* 29, 1038–1047. <https://doi.org/10.1111/1365-2435.12406>.
- Bull, J.J., 1980. Sex determination in reptiles. *Q. Rev. Biol.* 55, 3–21.
- Bull, C.M., Burzacott, D., 2002. Changes in climate and in the timing of pairing of the Australian lizard, *Tiliqua rugosa*: a 15-year study. *J. Zool.* 256, 383–387. <https://doi.org/10.1017/S0952836902000420>.
- Cabrelli, A.L., Stow, A.J., Hughes, L., 2014. A framework for assessing the vulnerability of species to climate change: a case study of the Australian elapid snakes. *Biodivers. Conserv.* 23, 3019–3034. <https://doi.org/10.1007/s10531-014-0760-0>.
- Cahill, A.E., Aiello-Lammens, M.E., Fisher-Reid, M.C., Hua, X., Karanewsky, C.J., Yeong Ryu, H., Sbeglia, G.C., Spagnolo, F., Waldron, J.B., Warsi, O., Wiens, J.J., 2013. How does climate change cause extinction? *Proc. R. Soc. Lond. B* 280, 20121890. <https://doi.org/10.1098/rspb.2012.1890>.
- Caldwell, A.J., While, G.M., Beeton, N.J., Wapstra, E., 2015. Potential for thermal tolerance to mediate climate change effects on three members of a cool temperate lizard genus, *Niveoscincus*. *J. Therm. Biol.* <https://doi.org/10.1016/j.jtherbio.2015.05.002>.
- Capula, M., Rugiero, L., Capizzi, D., Milana, G., Vignoli, L., Franco, D., Petrozzi, F., Luiselli, L., 2014. Long-term, climate change-related shifts in monthly patterns of roadkilled Mediterranean snakes (*Hierophis viridiflavus*). *Herpetol. J.* 24, 97–102.
- Capula, M., Rugiero, L., Capizzi, D., Franco, D., Milana, G., Luiselli, L., 2015. Long-term, climate-change-related shifts in feeding frequencies of a Mediterranean snake population. *Ecol. Res.* <https://doi.org/10.1007/s11284-015-1312-0>.
- Carlo, M.A., Riddell, E.A., Levy, O., Sears, M.W., 2017. Recurrent sublethal warming reduces embryonic survival, inhibits juvenile growth, and alters species distribution projections under climate change. *Ecol. Lett.* <https://doi.org/10.1111/ele.12877>.
- Carvalho, S.B., Brito, J.C., Crespo, E.J., Possingham, H., 2010. From climate change predictions to actions – conserving vulnerable animal groups in hotspots at a regional scale. *Glob. Change Biol.* 16, 3257–3270. <https://doi.org/10.1111/j.1365-2486.2010.02212.x>.
- Caten, C.T., Lima-Ribeiro, M.S., Silva Jr, N.J., Moreno, A.K., Terrible, L.C., 2017. Evaluating the effectiveness of Brazilian protected areas under climate change: a case study of *Micrurus brasiliensis* (Serpentes: elapidae). *Trop. Conserv. Sci.* 10, 1–8. <https://doi.org/10.1177/1940082917722027>.
- Ceia-Hasse, A., Sinervo, B., Vicente, L., Pereira, H.M., 2014. Integrating ecophysiological models into species distribution projections of European reptile range shifts in response to climate change. *Ecography* 37, 1–10. <https://doi.org/10.1111/j.1600-0587.2013.00600.x>.
- Chamaillé-Jammes, S., Massot, M., Arangón, P., Clobert, J., 2006. Global warming and positive fitness response in mountain populations of common lizards *Lacerta vivipara*. *Glob. Change Biol.* 12, 392–402. <https://doi.org/10.1111/j.1365-2486.2005.01088.x>.
- Chevin, L.M., Lande, R., Mace, G.M., 2010. Adaptation, plasticity and extinction in a changing environment: towards a predictive theory. *PLoS Biol.* 8 (4). <https://doi.org/10.1371/journal.pbio.1000357>. e1000357.
- Clark, R.W., Marchand, M.N., Clifford, B.J., Stechert, R., Stephens, S., 2011. Decline of an isolated timber rattlesnake (*Crotalus horridus*) population: interactions between climate change, disease, and loss of genetic diversity. *Biol. Conserv.* 144, 886–891.
- Clarke, D.N., Zani, P.A., 2012. Effects of night-time warming on temperate ectotherm reproduction: potential fitness benefits of climate change for side-blotched lizards. *J. Exp. Biol.* 215, 1117–1127. <https://doi.org/10.1242/jeb.065359>.
- Clusella-Trullas, S., Blackburn, T.M., Chown, S.L., 2011. Climatic predictors of temperature performance curve parameters in ectotherms imply complex responses to climate change. *Am. Nat.* 177, 738–751. <https://doi.org/10.1086/660021>.
- Clusella-Trullas, S., Chown, S.L., 2014. Lizard thermal trait variation at multiple scales: a review. *J. Comp. Physiol. B* 184, 5–21. <https://doi.org/10.1007/s00360-013-0776-x>.
- Collins, M., Knutti, R., Arblaster, J., Dufresne, J.-L., Fichet, T., Friedlingstein, P., Gao, X., Gutowski, W.J., Johns, T., Krinner, G., Shongwe, M., TEBaldi, C., Weaver, A.J., Wehner, M., 2013. Long-term climate change: projections, commitments and irreversibility. In: Stocker, T.F., Qin, D., Plattner, G.-K., Tignor, M., Allen, S.K., Boschung, J., Nauels, A., Xia, Y., Bex, V., Midgley, P.M. (Eds.), *Climate Change 2013: The Physical Science Basis. Contribution of Working Group I to the Fifth Assessment Report of the Intergovernmental Panel on Climate Change*. Cambridge University Press, Cambridge, United Kingdom and New York, NY, USA.
- Boschung, J., Nauels, A., Xia, Y., Bex, V., Midgley, P.M. (Eds.), *Climate Change 2013: The Physical Science Basis. Contribution of Working Group I to the Fifth Assessment Report of the Intergovernmental Panel on Climate Change*. Cambridge University Press, Cambridge, United Kingdom and New York, NY, USA.
- Cooper, A., Turney, C., Hughton, K.A., Brook, B.W., Mcdonald, H.G., Bradshaw, C.J.A., 2015. Abrupt warming events drove Late Pleistocene Holarctic megafaunal turnover. *Science* 349, 602–606.
- Cowles, R.B., Bogert, C.M., 1944. A preliminary study of the thermal requirements of desert reptiles. *Bull. Am. Mus. Nat. Hist.* 83, 265–296.
- Cox, W.A., Thompson, F.R., Reidy, J.L., 2013. The effects of temperature on nest predation by mammals, birds, and snakes. *Auk* 130, 784–790. <https://doi.org/10.1525/auk.2013.13033>.
- Cubasch, U., Wuebbles, D., Chen, D., Facchini, M.C., Frame, D., Mahowald, N., Winther, J.-G., 2013. Introduction. In: Stocker, T.F., Qin, D., Plattner, G.-K., Tignor, M., Allen, S.K., Boschung, J., Nauels, A., Xia, Y., Bex, V., Midgley, P.M. (Eds.), *Climate Change 2013: The Physical Science Basis. Contribution of Working Group I to the Fifth Assessment Report of the Intergovernmental Panel on Climate Change*. Cambridge University Press, Cambridge, United Kingdom and New York, NY, USA.
- Cunningham, G.D., While, G.M., Wapstra, E., 2017. Climate and sex ratio variation in a viviparous lizard. *Biol. Lett.* 13, 2017218. <https://doi.org/10.1098/rsbl.2017.0218>.
- Davis, M.A., Douglas, M.R., Webb, C.T., Collyer, M.L., Holycross, A.T., Painter, C.W., Kamees, L.K., Douglas, M.E., 2015. Nowhere to go but up: impacts of climate change on demographics of a short-range endemic (*Crotalus willardi obscurus*) in the sky-islands of southwestern North America. *PLoS One* 10 (6), e0131067. <https://doi.org/10.1371/journal.pone.0131067>.
- Dawson, T.P., Jackson, S.T., House, J.I., Prentice, I.C., Mace, G.M., 2011. Beyond predictions: biodiversity conservation in a changing climate. *Science* 332, 53–58.
- Dayananda, B., Webb, J.K., 2017. Incubation under climate warming affects learning ability and survival in hatchling lizards. *Biol. Lett.* 13, 20170002. <https://doi.org/10.1098/rsbl.2017.0002>.
- Dayananda, B., Gray, S., Pike, D., Webb, J.K., 2016. Communal nesting under climate change: fitness consequences of higher incubation temperatures for a nocturnal lizard. *Glob. Change Biol.* 22, 2405–2414. <https://doi.org/10.1111/gcb.13231>.
- Dayananda, B., Murray, B.R., Webb, J.K., 2017. Hotter nests produce hatchling lizards with lower thermal tolerance. *J. Exp. Biol.* 220, 2159–2165. <https://doi.org/10.1242/jeb.152272>.
- DeGregorio, B.A., Westervelt, J.D., Weatherhead, P.J., Sperry, J.H., 2015. Indirect effect of climate change: shifts in ratsnake behavior alter intensity and timing of avian nest predation. *Ecol. Model.* 312, 239–246. <https://doi.org/10.1016/j.ecolmodel.2015.05.031>.
- Diele-Viegas, L.M., Vitt, L.J., Sinervo, B., Colli, G.R., Werneck, F.P., Miles, D.B., Magnusson, W.E., Santos, J.C., Sette, C.M., Caetano, G.H.O., Pontes, E., Ávila-Pires, T.C.S., 2018. Thermal physiology of Amazonian lizards (Reptilia: squamata). *PLoS One* 13 (3), e0192834. <https://doi.org/10.1371/journal.pone.0192834>.
- Doody, J.S., Guarino, E., Georges, A., Corey, B., Murray, G., Ewert, M., 2006. Nest site choice compensates for climate effects on sex ratios in a lizard with environmental sex determination. *Evolut. Ecol.* 20, 307–330. <https://doi.org/10.1007/s10682-006-0003-2>.
- Dubey, S., Shine, R., 2011. Predicting the effects of climate change on reproductive fitness of an endangered montane lizard, *Eulamprus leuraensis* (Scincidae). *Clim. Change* 107, 531–547. <https://doi.org/10.1007/s10584-010-9963-x>.
- Dubey, S., Pike, D.A., Shine, R., 2013. Predicting the impacts of climate change on genetic diversity in an endangered lizard species. *Clim. Change* 117, 319–327. <https://doi.org/10.1007/s10584-012-0540-3>.
- DuBois, P.M., Shea, T.K., Claunch, N.M., Taylor, E.N., 2017. Effects of oxygen on responses to heating in two lizard species sampled along an elevational gradient. *J. Therm. Biol.* <https://doi.org/10.1016/j.jtherbio.2017.02.008>.
- Dunham, A.E., Grant, B.W., Overall, K.L., 1989. Interfaces between biophysical and physiological ecology and the population ecology of terrestrial vertebrate ectotherms. *Physiol. Zool.* 62, 335–355.
- Dupoué, A., Rutschmann, A., Le Galliard, J.F., Miles, D.B., Clobert, J., DeNardo, D.F., Brusch IV, G.A., Meylan, S., 2017a. Water availability and environmental temperature correlate with geographic variation in water balance in common lizards. *Oecologia* 185, 561–571. <https://doi.org/10.1007/s00442-017-3973-6>.
- Dupoué, A., Rutschmann, A., Le Galliard, J.F., Clobert, J., Angelier, F., Marciau, C., Ruault, S., Miles, D.B., Meylan, S., 2017b. Shorter telomeres precede population extinction in wild lizards. *Sci. Rep.* 7, 16976. <https://doi.org/10.1038/s41598-017-17323-z>.
- Dupoué, A., Brischoux, F., Lourdais, O., 2017c. Climate and foraging mode explain interspecific variation in snake metabolic rates. *Proc. R. Soc. B* 284, 20172108. <https://doi.org/10.1098/rspb.2017.2108>.
- Dupoué, A., Rutschmann, A., Le Galliard, J.F., Clobert, J., Blaimont, P., Sinervo, B., Miles, D.B., Haussy, C., Meylan, S., 2018. Reduction in baseline corticosterone secretion correlates with climate warming and drying across wild lizard populations. *J. Anim. Ecol.* 87, 1331–1341. <https://doi.org/10.1111/1365-2656.12843>.
- Ferri-Yáñez, F., Araújo, M.B., 2015. Lizards could be warming faster than climate. *Ecography* 38, 01–03. <https://doi.org/10.1111/ecog.01481>.
- Flato, G., Marotzke, J., Abiodun, B., Braconnot, P., Chou, S.C., Collins, W., Cox, P., Driouch, F., Emori, S., Eyring, V., Forest, C., Gleckler, P., Guilyardi, E., Jakob, C., Kattsov, V., Reason, C., Rummukainen, M., 2013. Evaluation of climate models. In: Stocker, T.F., Qin, D., Plattner, G.-K., Tignor, M., Allen, S.K., Boschung, J., Nauels, A., Xia, Y., Bex, V., Midgley, P.M. (Eds.), *Climate Change 2013: The Physical Science Basis. Contribution of Working Group I to the Fifth Assessment Report of the Intergovernmental Panel on Climate Change*. Cambridge University Press, Cambridge, United Kingdom and New York, NY, USA.
- Flesch, A.D., Rosen, P.C., Holm, P., 2017. Long-term changes in abundances of Sonorian

- Desert Lizards reveal complex responses to climatic variation. *Glob. Change Biol.* <https://doi.org/10.1111/gcb.13813>.
- Fordham, D.A., Watts, M.J., Delean, S., Brook, B.W., Heard, L.B., Bull, C.M., 2012. Managed relocation as an adaptation strategy for mitigating climate change threats to the persistence of an endangered lizard. *Glob. Change Biol.* 18, 2743–2755. <https://doi.org/10.1111/j.1365-2486.2012.02742.x>.
- Fordham, D.A., Saltré, F., Brown, S.C., Mellin, C., Wigley, T.M.L., 2017. Why decadal to century timescale paleoclimate data is needed to explain present-day patterns of biological diversity and change. *Glob. Change Biol.* <https://doi.org/10.1111/gcb.13932>.
- Gadsden, H., Ballasteros-Barrera, C., Garza, H.O., Castañeda, G., García-de la Peña, C., Lemos-Espinal, J.A., 2012. Effects of land-cover transformation and climate change on the distribution of two endemic lizards, *Crotaphytus antiquus* and *Sceloporus cyanostictus*, of northern Mexico. *J. Arid Environ.* 83, 1e9. <https://doi.org/10.1016/j.jaridenv.2012.03.014>.
- George, A.D., Thompson, F.R., Faaborg, J., 2015. Isolating weather effects from seasonal activity patterns of a temperate North American Colubrid. *Oecologia*. <https://doi.org/10.1007/s00442-015-3300-z>.
- George, A.D., Connette, G.M., Thompson, F.R., Faaborg, J., 2017. Resource selection by an ectothermic predator in a dynamic thermal landscape. *Ecol. Evol.* <https://doi.org/10.1002/ece3.3440>.
- Gilbert, A.L., Lattanzio, M.S., 2016. Ontogenetic variation in the thermal biology of Yarrow's Spiny lizard, *Sceloporus jarrovi*. *PLoS One* 11, e0146904. <https://doi.org/10.1371/journal.pone.0146904>.
- Gilbert, A.L., Miles, D.B., 2017. Natural selection on thermal performance, critical thermal maxima and locomotor performance. *Proc. R. Soc. B* 284, 20170536. <https://doi.org/10.1098/rspb.2017.0536>.
- Goller, M., Goller, F., French, S.S., 2014. A heterogeneous thermal environment enables remarkable behavioral thermoregulation in *Uta stansburiana*. *Ecol. Evol.* <https://doi.org/10.1002/ece3.1141>.
- Grayson, K.L., Mitchell, N.J., Monks, J.M., Keall, S.N., Wilson, J.N., Nelson, N.J., 2014. Sex ratio bias and extinction risk in an isolated population of tuatara (*Sphenodon punctatus*). *PLoS One* 9, e94214. <https://doi.org/10.1371/journal.pone.0094214>.
- Grimm-Seyfarth, A., Mihoub, J.B., Henle, K., 2017. Too hot to die? The effects of vegetation shading on past, present, and future activity budgets of two diurnal skinks from arid Australia. *Ecol. Evol.* <https://doi.org/10.1002/ece3.3238>.
- Gunderson, A.E., Leal, M., 2015. Patterns of thermal constraint on ectotherm activity. *Am. Nat.* 185, 653–664. <https://doi.org/10.5061/dryad.48vb7>.
- Gunderson, A.E., Leal, M., 2016. A conceptual framework for understanding thermal constraints on ectotherm activity with implications for predicting responses to global change. *Ecol. Lett.* 19, 111–120. <https://doi.org/10.1111/ele.12552>.
- Gunderson, A.E., Stillman, J.H., 2015. Plasticity in thermal tolerance has limited potential to buffer ectotherms from global warming. *Proc. R. Soc. B*. <https://doi.org/10.1098/rspb.2015.0401>.
- Gynther, I., Waller, N., Leung, L.K.-P., 2016. Confirmation of the Extinction of the Bramble Cay Melomys *Melomys rubicula* on Bramble Cay, Torres Strait: Results and Conclusions from a Comprehensive Survey in August–September 2014. Unpublished Report to the Department of Environment and Heritage Protection. Queensland Government, Brisbane.
- Haddock, C.K., Rindskopf, D., Shadish, W.R., 1998. Using odds ratios as effect sizes for Meta-Analysis of dichotomous data: a primer on methods and issues. *Psychol. Methods* 3, 339–353.
- Hansen, J.E., Sato, M., 2012. Paleoclimate implications for human-made climate change. In: *Climate Change*. Springer, Vienna, pp. 21–47.
- Hare, K.M., Cree, A., 2010. Exploring the consequences of climate-induced changes in cloud cover on offspring of a cool-temperate viviparous lizard. *Biol. J. Linn. Soc.* 101, 844–851.
- Hartmann, D.L., Klein Tank, A.M.G., Rusticucci, M., Alexander, L.V., Brönnimann, S., Charabi, Y., Dentener, F.J., Dlugokencky, E.J., Easterling, D.R., Kaplan, A., Soden, B.J., Thorne, P.W., Wild, M., Zhai, P.M., 2013. Observations: atmosphere and surface. In: Stocker, T.F., Qin, D., Plattner, G.-K., Tignor, M., Allen, S.K., Boschung, J., Nauels, A., Xia, Y., Bex, V., Midgley, P.M. (Eds.), *Climate Change 2013: The Physical Science Basis. Contribution of Working Group I to the Fifth Assessment Report of the Intergovernmental Panel on Climate Change*. Cambridge University Press, Cambridge, United Kingdom and New York, NY, USA.
- Hertz, P.E., Huey, R.B., Stenvenson, R.D., 1993. Evaluating temperature regulation by field-active ectotherms: the fallacy of an inappropriate question. *Am. Nat.* 142, 796–818. <https://doi.org/10.1086/285573>.
- Holt, B.G., Lessard, J.P., Borregaard, M.K., Fritz, S.A., Araújo, M.B., Dimitrov, D., Fabre, P.H., Graham, C.H., Graves, G.R., Jonsson, K.A., Nogués-Bravo, D., Wang, Z., Whittaker, R.J., Fjelds, J., Rahbek, C., 2012. An update of Wallace's zoogeographic regions of the world. *Science* 339, 74–77. <https://doi.org/10.1126/science.1228282>.
- Houniet, D.T., Thuiller, W., Tolley, K.A., 2009. Potential effects of predicted climate change on the endemic South African Dwarf Chameleons, *Bradypodion*. *Afr. J. Herpetol.* 58, 28–35.
- Huang, W.S., Pike, D.A., 2011. Climate change impacts on fitness depend on nesting habitat in lizards. *Funct. Ecol.* 25, 1125–1136. <https://doi.org/10.1111/j.1365-2435.2011.01855.x>.
- Huang, S.P., Chiou, C.R., Lin, T.E., Tu, M.C., Lin, C.C., Porter, W.P., 2013. Future advantages in energetics, activity time, and habitats predicted in a high-altitude pit viper with climate warming. *Funct. Ecol.* 27, 446–458. <https://doi.org/10.1111/1365-2435.12040>.
- Huang, S.P., Porter, W.P., Tu, M.C., Chiou, C.R., 2014a. Forest cover reduces thermally suitable habitats and affects responses to a warmer climate predicted in a high-elevation lizard. *Oecologia*. <https://doi.org/10.1007/s00442-014-2882-1>.
- Huang, Y., Wu, X., Hong Li, Y., Liao, W.B., 2014b. Global warming, body size and conservation in a Qinghai-Tibet Plateau lizard. *Herpetol. J.* 24, 161–165.
- Huey, R.B., 1982. Temperature, physiology and the ecology of reptiles. In: Gans, C., Pough, F.H. (Eds.), *Biology of Reptilia*, vol. 12. Physiological Ecology. 12. Academic Press, New York, pp. 25–91.
- Huey, R.B., Slatkin, M., 1976. Costs and benefits of lizard thermoregulation. *Q. Rev. Biol.* 51, 363–384.
- Huey, R.B., Deutsch, C.A., Tewksbury, J.J., Vitt, L.J., Hertz, P.E., Pérez, H.J.A., Garland Jr., T., 2009. Why tropical forest lizards are vulnerable to climate warming. *Proc. R. Soc. B*. <https://doi.org/10.1098/rspb.20081957>.
- Huey, R.B., Kearney, M.R., Krockenberger, A., Holtum, J.A.M., Jess, M., Williams, S.E., 2012. Predicting organismal vulnerability to climate warming: roles of behaviour, physiology and adaptation. *Philos. Trans. R. Soc. B* 367, 1665–1679. <https://doi.org/10.1098/rstb.2012.0005>.
- Jansson, R., 2003. Global patterns of endemism explained by past climatic change. *Proc. R. Soc. B* 270, 583590.
- Jarvie, S., Besson, A.A., Seddon, P.J., Cree, A., 2014. Assessing thermal suitability of translocation release sites for egg-laying reptiles with temperature-dependent sex determination: a case study with tuatara. *Anim. Conserv.* 17, 48–55. <https://doi.org/10.1111/acv.12152>.
- Jetz, W., Fine, P., 2012. Area and productivity of the world's biomes integrated over geological time predicts global patterns of vertebrate diversity. *PLoS Biol.* 10, e1001292.
- Jones, A.R., Bull, C.M., Brook, B.W., Wells, K., Pollock, K.H., Fordham, D.A., 2016. Tick exposure and extreme climate events impact survival and threaten the persistence of a long-lived lizard. *J. Anim. Ecol.* 85, 598–610.
- Kearney, M., 2013. Activity restriction and the mechanistic basis for extinctions under climate warming. *Ecol. Lett.* <https://doi.org/10.1111/ele.12192>.
- Kearney, M., Shine, R., Porter, M.R., 2009. The potential for behavioral thermoregulation to buffer “cold-blooded” animals against climate warming. *Proc. Nat. Acad. Sci. USA* 106, 3835–3840. <https://doi.org/10.073/pnas.0808913106>.
- Kirchoff, S., Heten, R.S., Lease, H.M., Miles, D.B., Mitchell, D., Müller, J., Rödel, M.O., Sinervo, B., Wassenaar, T., Murray, I.W., 2017. Thermoregulatory behavior and high thermal preference buffer impact of climate change in a Namib Desert Lizard. *Ecosphere* 8, e02033. <https://doi.org/10.1002/ecs2.2033>.
- Koumoundouros, T., Sumner, J., Clemann, N., Stuart-Fox, D., 2013. Current genetic isolation and fragmentation contrasts with historical connectivity in an alpine lizard (*Cyclodomorphus praealtus*) threatened by climate change. *Biol. Conserv.* <https://doi.org/10.1016/j.biocon.2008.12.026>.
- Kubisch, E.L., Piantoni, C., Williams, J., Scolaro, A., Navas, C.A., Ibarguengoytia, N., 2012. Do higher temperatures increase growth in the Nocturnal Gecko *Homonota darwini* (Gekkota: phyllodactylidae)? A skeletochronological assessment analyzed at temporal and geographic scales. *J. Herpetol.* 46, 587–595. <https://doi.org/10.1670/10-277>.
- Kubisch, E.L., Fernández, J.B., Ibarguengoytia, N.R., 2015. Vulnerability to climate warming of *Liolaemus pictus* (Squamata, Liolaemidae), a lizard from the cold temperate climate in Patagonia, Argentina. *J. Comp. Physiol. B*. <https://doi.org/10.1007/s00360-015-0952-2>.
- Kubisch, E.L., Corbálan, V., Ibarguengoytia, N.R., Sinervo, B., 2016. Local extinction risk of three species of lizard from Patagonia as a result of global warming. *Can. J. Zool.* 94, 49–59. <https://doi.org/10.1139/cjz-2015-0024>.
- Lane, D.M., 2018. Online Statistics Education: A Multimedia Course of Study. Rice University, United States (Accessed 25 June 2018). <http://onlinestatbook.com/>.
- Lawing, A.M., Polly, P.D., 2011. Pleistocene climate, phylogeny, and climate envelope models: an integrative approach to better understand species' response to climate change. *PLoS One* 6 (12), e28554. <https://doi.org/10.1371/journal.pone.0028554>.
- Leal, M., Gunderson, A., 2012. Rapid change in the thermal tolerance of a tropical lizard. *Am. Nat.* 180, 815–822.
- Leadley, P., Pereira, H.M., Alkemade, R., Fernandez-Manjarres, J.F., Proenca, V., Scharelemann, J.P.W., Walpole, M.J., 2010. Biodiversity scenarios: projections of 21st century change in biodiversity and associated ecosystem services. In: Diversity, SotCoB (Ed.), *Secretariat of the Convention on Biological Diversity (Technical Series no. 50)*. Published by the Secretariat of the Convention on Biological Diversity, Montreal, pp. 1–132.
- Lelièvre, H., Rivalan, P., Delmas, V., Ballouard, J.M., Bonnet, J., Blouin-Demers, G., Lourdaux, O., 2013. The thermoregulatory strategy of two sympatric colubrid snakes affects their demography. *Popul. Ecol.* 55, 585–593.
- Lepetz, V., Massot, M., Chaine, A., Clobert, J., 2009. Climate warming and the evolution of morphotypes in a reptile. *Glob. Change Biol.* 15, 454–466. <https://doi.org/10.1111/j.1365-2486.2008.01761.x>.
- Levy, O., Buckley, L.B., Keitt, T.H., Smith, C.D., Boateng, K.O., Kumar, D.S., Angilletta Jr., M.J., 2015. Resolving the life cycles alters expected impacts of climate change. *Proc. R. Soc. B* 282, 20150837. <https://doi.org/10.1098/rspb.2015.0837>.
- Levy, O., Buckley, L.B., Keitt, T.H., Angilletta Jr., M.J., 2016. Ontogeny constrains phenology: opportunities for activity and reproduction interact to dictate potential phenologies in a changing climate. *Ecol. Lett.* 19, 620–628. <https://doi.org/10.1111/ele.12595>.
- Levy, O., Borchert, J.D., Rusch, T.W., Buckley, L.B., Angilletta Jr., M.J., 2017. Diminishing returns limit energetic costs of climate change. *Ecology* 98, 1217–1228. <https://doi.org/10.1002/ecy.1803>.
- Li, S.R., Wang, Y., Ma, L., Zeng, Z.G., Bi, J.H., 2017. Thermal ecology of three coexistent desert lizards: implications for habitat divergence and thermal vulnerability. *J. Comp. Physiol. B*. <https://doi.org/10.1007/s00360-017-1087-4>.
- Lipsey, Mark W., Wilson, David B., 2001. *Practical Meta-Analysis*. Sage Publications, Inc., Thousand Oaks, California, United States.
- Ljungström, G., Wapstra, E., Olsson, M., 2015. Sand lizard (*Lacerta agilis*) phenology in a warming world. *Evolut. Biol.* 15, 206. <https://doi.org/10.1186/s12862-015-0476-0>.



- Llewellyn, J., Macdonald, S.L., Hatcher, A., Moritz, C., Philips, B.L., 2016. Intraspecific variation in climate-relevant traits in a tropical rainforest lizard. *Divers. Distrib.* <https://doi.org/10.1111/ddi.12466>.
- Llewellyn, J., Macdonald, S.L., Hatcher, A., Moritz, C., Philips, B.L., 2017. Thermoregulatory behaviour explains countergradient variation in the upper thermal limit of a rainforest skink. *Oikos* 126 (5), 748–757. <https://doi.org/10.1111/oik.03933>.
- Logan, M.L., Huynh, R.K., Precious, R.A., Calsbeek, R.G., 2013. The impact of climate change measured at relevant spatial scales: new hope for tropical lizards. *Glob. Change Biol.* <https://doi.org/10.1111/gcb.12253>.
- Logan, M.L., Cox, R.M., Calsbeek, R., 2014. Natural selection on thermal performance in a novel thermal environment. *Proc. Nat. Acad. Sci. USA* 111, 14165–14169. <https://doi.org/10.1073/pnas.1404885111>.
- Logan, M.L., Fernandez, S.G., Calsbeek, R., 2015. Abiotic constraints on the activity of tropical lizards. *Funct. Ecol.* 29, 694–700. <https://doi.org/10.1111/1365-2435.12379>.
- López-Alcaide, S., Nakamura, M., Smith, E.N., Martínez-Meyer, E., 2017. Would behavioral thermoregulation enables pregnant viviparous tropical lizards to cope with a warmer world? *Integr. Zool.* 12, 379–395. <https://doi.org/10.1111/1749-4877.12253>.
- Lourdais, O., Shine, R., Bonnet, X., Guillon, M., Guy, N., 2004. Climate affects embryonic development in a viviparous snake, *Vipera aspis*. *Oikos* 104, 551–560.
- Lu, H., Wang, Y., Tang, W., Du, W., 2013. Experimental evaluation of reproductive response to climate warming in an oviparous skink. *Integr. Zool.* 8, 175–183. <https://doi.org/10.1111/1749-4877.12025>.
- Mace, G.M., Collar, N.J., Gaston, K.J., Hilton-Taylor, C., Akçakaya, H.R., Leader-Williams, N., Milner-Gulland, E.J., Stuart, S.N., 2008. Quantification of extinction risk: IUCN's system for classifying threatened species. *Conserv. Biol.* 22, 1424–1442. <https://doi.org/10.1111/j.1523-1739.2008.01044.x>.
- Marquis, O., Massot, M., Le Galliard, J.F., 2008. Intergenerational effects of climate generate cohort variation in lizard reproductive performance. *Ecology* 89, 2575–2583.
- Martín, J., López, P., 2013. Effects of global warming on sensory ecology of rock lizards: increased temperatures alter the efficacy of sexual chemical signals. *Funct. Ecol.* <https://doi.org/10.1111/1365-2435.12128>.
- Martínez-Freiría, F., Argaz, H., Fahd, S., Brito, J.S., 2013. Climate change is predicted to negatively influence Moroccan endemic reptile richness. Implications for conservation in protected areas. *Naturwissenschaften* 100, 877–889. <https://doi.org/10.1007/s00114-013-1088-4>.
- Martínez-Méndez, N., Mejía, O., Cruz, F.R.M., 2015. The past, present and future of a lizard: the phylogeography and extinction risk of *Sceloporus serrifer* (Squamata: phrynosomatidae) under a global warming scenario. *Zool. Anz.* 254, 86–98. <https://doi.org/10.1016/j.jcz.2014.12.004>.
- Massot, M., Clobert, J., Ferrière, R., 2008. Climate warming, dispersal inhibition and extinction risk. *Glob. Change Biol.* 14, 461–469. <https://doi.org/10.1111/j.1365-2486.2007.01514.x>.
- Massot, M., Legendre, S., Fédéric, P., Clobert, J., 2017. Climate warming: a loss of variation in populations can accompany reproductive shifts. *Ecol. Lett.* <https://doi.org/10.1111/ele.12811>.
- McCarty, J.P., 2001. Ecological consequences of recent climate change. *Conserv. Biol.* 15, 320–331.
- Medina, M., Sclaro, A., Méndez-de la Cruz, F., Sinervo, B., Miles, D.B., Ibarguengoytia, N., 2012. Thermal biology of the genus *Lialemus*: a phylogenetic approach reveals advantages of the genus to survive climate change. *J. Therm. Biol.* 37, 579–586. <https://doi.org/10.1016/j.jthermbio.2012.06.006>.
- Medina, M., Fernández, J.B., Charruau, P., Méndez de la Cruz, F., Ibarguengoytia, N., 2016. Vulnerability to climate change of *Anolis allisoni* in the mangrove habitats of Banco Chochorro Islands, Mexico. *J. Therm. Biol.* 58, 8–14. <https://doi.org/10.1016/j.jthermbio.2016.02.005>.
- Meiri, S., Bauer, A.M., Chirio, L., Colli, G.R., Das, I., Doan, T.M., Feldman, A., Herrera, F.C., Novosolov, M., Pafilis, P., Pinchera-Donoso, D., Powney, G., Torres-Carvajal, O., Uetz, P., Van Damme, R., 2013. Are lizards feeling the heat? A tale of ecology and evolution under two temperatures. *Glob. Ecol. Biogeogr.* 22, 834–845. <https://doi.org/10.1111/geb.12053>.
- Meng, H., Carr, J., Beraducci, J., Bowles, B., Branch, W.R., Capitani, C., Cheng, J., Cox, N., Howell, K., Malonza, P., Marchant, R., Burgess, N.D., et al., 2016. Tanzania's reptile biodiversity: distribution, threats and climate change vulnerability. *Biol. Conserv.* 204, 72–82. <https://doi.org/10.1016/j.biocon.2016.04.008>.
- Meylan, S., Miles, D.B., Clobert, J., 2012. Hormonally mediated maternal effects, individual strategy and global change. *Philos. Trans. R. Soc. B* 367, 1647–1664. <https://doi.org/10.1098/rstb.2012.0020>.
- Miller, K.A., Miller, H.C., Moore, J.A., Mitchell, N.J., Cree, A., Allendorf, F.W., Sarre, S.D., Keall, S.N., Nelson, N.J., 2012. Securing the Demographic and Genetic Future of Tuatara through Assisted Colonization. *Conserv. Biol.* 26, 790–798. <https://doi.org/10.1111/j.1523-1739.2012.01902.x>.
- Minoli, I., Avila, L.J., 2017. Conservation assessments in climate change scenarios: spatial perspectives for present and future in two *Pristidactylus* (Squamata: leiosauridae) lizards from Argentina. *Zootaxa* 4237, 091–111. <https://doi.org/10.11646/zootaxa.4237.1.5>.
- Mitchell, N.J., Kearney, M.R., Nelson, N.J., Porter, W., 2008. Predicting the fate of a living fossil: how will global warming affect sex determination and hatching phenology in tuatara? *Proc. R. Soc. B* 275, 2185–2193. <https://doi.org/10.1098/rspb.2008.0438>.
- Mitchell, N.J., Allendorf, F.W., Keall, S.N., Daugherty, C.H., Nelson, N.J., 2010. Demographic effects of temperature-dependent sex determination: will tuatara survive global warming? *Glob. Change Biol.* 16, 60–72. <https://doi.org/10.1111/j.1365-2486.2009.01964.x>.
- Monasterio, C., Shoo, L.P., Salvador, A., Iraeta, P., Díaz, J.A., 2013. High temperature constrains reproductive success in a temperate lizard: implications for distribution range limits and the impacts of climate change. *J. Zool.* <https://doi.org/10.1111/jzo.12057>.
- Moreno-Rueda, G., Pleguezuelos, J.M., Alaminos, E., 2009. Climate warming and activity period extension in the Mediterranean snake *Malpolon monspessulanus*. *Clim. Change* 92, 235–242. <https://doi.org/10.1007/s10584-008-9469-y>.
- Moritz, C., Langham, G., Kearney, M., Krockenberger, A., VanDerWal, J., Williams, S., 2012. Integrating phylogeography and physiology reveals divergence of thermal traits between central and peripheral lineages of tropical rainforest lizards. *Philos. Trans. R. Soc. B* 367, 1680–1687. <https://doi.org/10.1098/rstb.2012.0018>.
- Munigua-Vega, A., Rodríguez-Estrella, R., Shaw, W.W., Culver, M., 2013. Localized extinction of an arboreal desert lizard caused by habitat fragmentation. *Biol. Conserv.* 157, 11–20. <https://doi.org/10.1016/j.biocon.2012.06.026>.
- Muñoz, M.M., Langham, G.M., Brandley, M.C., Rosauer, D.F., Williams, S.E., Moritz, C., 2016. Basking behavior predicts the evolution of heat tolerance in Australian rainforest lizards. *Evolution*. <https://doi.org/10.1111/evo.13064>.
- Nasrabadi, R., Rastegar-Pouyani, N., Rastegar-Pouyani, E., Kami, H.G., Gharzi, A., Yousefkhani, S.H., 2017. The effects of climate change on the distribution of European glass lizard *Pseudopus apodus* (PALLAS, 1775) in Eurasia. *Ecol. Res.* 1–6. <https://doi.org/10.1007/s11284-017-1530-8>.
- Naya, D.E., Veloso, C., Sabat, P., Bozinovic, F., 2011. Physiological flexibility and climate change: The case of digestive function regulation in lizards. *Comp. Biochem. Physiol. Part A: Mol. Integr. Physiol.* 159 (1), 100–104.
- Nelson, N.J., Keall, S.N., Pledger, S., Daugherty, C.H., 2002. Male-biased sex ratio in a small tuatara population. *J. Biogeogr.* 29, 633–640.
- Nelson, N.J., Thompson, M.B., Pledger, S., Keall, S.N., Daugherty, C.H., 2004. Do TSD, sex ratios, and nest characteristics influence the vulnerability of tuatara to global warming? *Int. Congr. Ser.* 1275, 250–257. <https://doi.org/10.1016/j.ics.2004.08.093>.
- Noble, D.W.A., Stenhouse, V., Schwanz, L.E., 2017. Developmental temperatures and phenotypic plasticity in reptiles: a systematic review and meta-analysis. *Biol. Rev.* <https://doi.org/10.1111/brev.12333>.
- Nori, J., Carrasco, P.A., Leynaud, G.C., 2014. Venomous snakes and climate change: ophidism as a dynamic problem. *Clim. Change* 122, 67–80. <https://doi.org/10.1007/s10584-013-1019-6>.
- Nori, J., Leynaud, G.C., Volante, J., Abdala, C.S., Scrocchi, G.J., Rodríguez-Soto, C., Pressey, R.L., Loyola, R., 2017. Reptile species persistence under climate change and direct human threats in north-western Argentina. *Environ. Conserv.* 1–7. <https://doi.org/10.1017/S0376892917000285>.
- Ofori, B.Y., Stow, A.J., Baumgartner, J.B., Beaumont, L.J., 2017. Combining dispersal, landscape connectivity and habitat suitability to assess climate induced changes in the distribution of Cunningham's skink, *Egernia cunninghami*. *PLoS One* 12, e0184193. <https://doi.org/10.1371/journal.pone.0184193>.
- Olsson, M., Schwartz, T., Wapstra, E., Uller, T., Ujvari, B., Madsen, T., Shine, R., 2011. Climate change, multiple paternity and offspring survival in lizards. *Evolution* 65, 3323–3326. <https://doi.org/10.1111/j.1558-5646.2011.01387.x>.
- Ortega, Z., Mencía, A., Pérez-Mellado, V., 2016a. Wind constraints on the thermoregulation of high mountain lizards. *Int. J. Biometeorol.* <https://doi.org/10.1007/s00484-016-1233-9>.
- Ortega, Z., Mencía, A., Pérez-Mellado, V., 2016b. Behavioral buffering of global warming in a cold-adapted lizard. *Ecol. Evol.* 6, 4582–4590. <https://doi.org/10.1002/ece3.2216>.
- Ortega, Z., Mencía, A., Pérez-Mellado, V., 2016c. The peak of thermoregulation effectiveness: thermal biology of the Pyrenean rock lizard, *Iberolacerta bonnali* (Squamata, Lacertidae). *J. Therm. Biol.* 56, 77–83. <https://doi.org/10.1016/j.jtherbio.2016.01.005>.
- Ortega, Z., Mencía, A., Pérez-Mellado, V., 2016d. Are mountain habitats becoming more suitable for generalist than cold-adapted lizards thermoregulation? *PeerJ* 4, e2085. <https://doi.org/10.7717/peerj.2085>.
- Park, J., Kim, H., Fong, J.J., Koo, K.S., Choi, W.J., Tsai, T.S., Park, D., 2017. Northward dispersal of sea kraits (*Laticauda semifasciata*) beyond their typical range. *PLoS One* 12, e0179871. <https://doi.org/10.1371/journal.pone.0179871>.
- Paranipe, D.A., Bastiaans, E., Patten, A., Cooper, R.D., Sinervo, B., 2013. Evidence of maternal effects on temperature preference in side-blotched lizards: implications for evolutionary response to climate change. *Ecol. Evol.* 3, 1977–1991. <https://doi.org/10.1002/ece3.614>.
- Peñuelas, J., Sardans, J., Estiarte, M., Ogaya, R., Carnicer, J., Coll, M., Barbeta, A., Rivas-Ubach, A., Llusià, J., Garbulska, M., Filella, I., Jump, A.S., 2013. Evidence of current impact of climate change on life: a walk from genes to the biosphere. *Glob. Change Biol.* 19 (8), 2303–2338.
- Piantoni, C., Navas, C.A., Ibarguengoytia, N.R., 2015. Vulnerability to climate warming of four genera of new world iguanians based on their thermal ecology. *Anim. Conserv.* <https://doi.org/10.1111/acv.12255>.
- Pincebourde, S., Murdock, C.C., Vickers, M., Sears, M.W., 2016. Fine-scale microclimatic variation can shape the responses of organisms to global change in both natural and urban environments. *Integr. Comp. Biol.* 56, 45–61. <https://doi.org/10.1093/icb/icw016>.
- Pinchera-Donoso, D., Tregenza, T., Witt, M.J., Hodgson, D.J., 2013. The evolution of viviparity opens opportunities for lizard radiation but drives it into a climatic cul-de-sac. *Glob. Ecol. Biogeogr.* 22, 857–867. <https://doi.org/10.1111/geb.12052>.
- Pintor, A.F.V., Schwarzkopf, L., Krockenberger, A.K., 2016. Oecologia. <https://doi.org/10.1007/s00442-016-3687-1>.
- Pomara, L.Y., Ledee, O.E., Martin, K.J., Zuckerman, B., 2014. Demographic consequences of climate change and land cover help explain a history of extirpations and range contraction in a declining snake species. *Glob. Change Biol.* <https://doi.org/10.1111/gcb.12052>.



- 1111/gcb.12510.
- Popescu, V.D., Rozyłowicz, L., Cogălniceanu, D., Niculae, I.M., Cucu, A.L., 2013. Moving into protected areas? Setting conservation priorities for Romanian reptiles and amphibians at risk from climate change. *PLoS One* 8, e79330. <https://doi.org/10.1371/journal.pone.0079330>.
- Pounds, J.A., Fodgen, M.P.L., Campbell, J.H., 1999. Biological responses to climate change on a tropical mountain. *Nature* 398, 611–615.
- Prates, I., Xue, A.T., Brown, J.L., Alvarado-Serrano, D.F., Rodrigues, M.T., Hickerson, M.J., Carnaval, A.C., 2016. Inferring responses to climate dynamics from historical demography in neotropical forest lizards. *Proc. Nat. Acad. Sci. USA*. <https://doi.org/10.1073/pnas.1601063113>.
- Prodon, R., Geniez, P., Cheylan, M., Devers, F., Chuine, I., Besnard, A., 2017. A reversal of the shift towards earlier spring phenology in several Mediterranean reptiles and amphibians during the 1998–2013 warming slowdown. *Glob. Change Biol.* 23, 5481–5491. <https://doi.org/10.1111/gcb.13812>.
- Putnam, B.J., Clark, R.W., 2017. Behavioral thermal tolerances of free-ranging rattlesnakes (*Crotalus oreganus*) during the summer foraging season. *J. Therm. Biol.* 65, 8–15. <https://doi.org/10.1016/j.jtherbio.2017.01.012>.
- R Core Team, 2017. R: A Language and Environment for Statistical Computing. Foundation for Statistical Computing, Austria. <https://www.R-project.org/>.
- Rabosky, A.R.D., Cori, A., Liwanag, H.E.M., Surget-GROBA, Y., Sinervo, B., 2012. Direct Fitness Correlates and Thermal Consequences of Facultative Aggregation in a Desert Lizard. *PLoS ONE* 7 (7). <https://doi.org/10.1371/journal.pone.0040866>. e40866.
- Rodda, G.H., Jarnevich, C.S., Reed, R.N., 2009a. What parts of the US mainland are climatically suitable for invasive alien pythons spreading from Everglades National Park? *Biol. Invasions* 11, 241–252. <https://doi.org/10.1007/s10530-008-9228-z>.
- Rödler, D., Schulte, U., 2010. Potential loss of genetic variability despite well established network of reserves: the case of the Iberian endemic lizard *Lacerta schreiberi*. *Biodivers. Conserv.* 19, 2651–2666. <https://doi.org/10.1007/s10531-010-9865-2>.
- Rodríguez, A., Rusciano, T., Hamilton, R., Holmes, L., Jordan, D., Valero, K.C.K., 2017. Genomic and phenotypic signatures of climate adaptation in an Anolis lizard. *Ecol. Evol.* 2017, 1–14. <https://doi.org/10.1002/ecs3.2985>.
- Romero-Díaz, C., Breedveld, M.C., Fitze, P.S., 2017. Climate effects on growth, body condition, and survival depend on the genetic characteristics of the population. *Am. Nat.* 190. <https://doi.org/10.1086/693780>.
- Rout, T.M., McDonald-Madden, E., Martin, T.G., Mitchell, N.J., Possingham, H.P., Armstrong, D.P., 2013. How to decide whether to move species threatened by climate change. *PLoS One* 8, e75814. <https://doi.org/10.1371/journal.pone.0075814>.
- Rugiero, L., Milana, G., Capula, M., Amori, G., Luiselli, L., 2012. Long term variations in small mammal composition of a snake diet do not mirror climate change trends. *Acta Oecol.* 43, 158–164. <https://doi.org/10.1016/j.actao.2012.07.002>.
- Rugiero, L., Milana, G., Petrozzi, F., Capula, M., Luiselli, L., 2013. Climate-change-related shifts in annual phenology of a temperate snake during the last 20 years. *Acta Oecol.* 51, 42–48. <https://doi.org/10.1016/j.actao.2013.05.005>.
- Salgado, J.F., 2018. Transforming the area under the normal curve (AUC) into Cohen's d, Pearson's rpb, odds-ratio, and natural log odds-ratio: two conversion tables. *Eur. J. Psychol. Appl. Leg. Context* 10 (1), 35–47. <https://doi.org/10.5093/ejpalc2018a5>.
- Sandel, B., Arge, L., Dalsgaard, B., Davies, R.G., Gaston, K.J., Sutherland, W.J., Svenning, J.C., 2011. The influence of late quaternary climate-change velocity on species endemism. *Science* 334, 660–664. <https://doi.org/10.1126/science.1210173>.
- Seddon, A.W., Macias-Fauria, M., Long, P.R., Benz, D., Willis, K.J., 2016. Sensitivity of global terrestrial ecosystems to climate variability. *Nature* 531, 229–232.
- Segall, M., Tolley, K.A., Vanhooydonck, B., Measey, G.J., Herrel, A., 2013. Impact of temperature on performance in two species of South African dwarf chameleon, *Bradypodion pumilum* and *B. occidentale*. *J. Exp. Biol.* 216, 3828–3836. <https://doi.org/10.1242/jeb.092353>.
- Settele, J., Scholes, R., Betts, R., Bunn, S., Leadley, P., Nepstad, D., Overpeck, J.T., Taboada, M.A., 2014. Terrestrial and inland water systems. In: Field, C.B., Barros, V.R., Dokken, D.J., Mach, K.J., Mastrandrea, M.D., Bilir, T.E., Chatterjee, M., Ebi, K.L., Estrada, Y.O., Genova, R.C., Girma, B., Kissel, E.S., Levy, A.N., MacCracken, S., Mastrandrea, P.R., White, L.L. (Eds.), *Climate Change 2014: Impacts, Adaptation, and Vulnerability. Part A: Global and Sectoral Aspects. Contribution of Working Group II to the Fifth Assessment Report of the Intergovernmental Panel on Climate Change*. Cambridge University Press, Cambridge, United Kingdom and New York, NY, USA, pp. 271–359.
- Scheffers, B.R., Edwards, D.P., Diesmos, A., Williams, S.E., Evans, T.A., 2014. Microhabitats reduce animal's exposure to climate extremes. *Glob. Change Biol.* 20, 495–503. <https://doi.org/10.1111/gcb.12439>.
- Sillero, N., Carretero, M.A., 2013. Modelling the past and future distribution of contracting species. The Iberian lizard *Podarcis carbonelli* (Squamata: lacertidae) as a case study. *Zool. Anz.* 252, 289–298. <https://doi.org/10.1016/j.jcz.2012.08.004>.
- Simoniello, P., Esposito, M.G., Trinchella, F., Motta, C.M., Scudiero, R., 2016. Alterations in brain morphology and HSP70 expression in lizard embryos exposed to thermal stress. *Comptes Rendus Biol.* <https://doi.org/10.1016/j.crvi.2016.07.002>.
- Sinclair, B.J., Marshall, K.E., Sewell, M.A., Levesque, D.L., Willett, C.S., Slotsbo, S., Dong, Y., Harley, C.D.G., Marshall, D.J., Helmut, B.S., Huey, R.B., 2016. Can we predict ectotherm responses to climate change using thermal performance curves and body temperatures? *Ecol. Lett.* 19, 1372–1385. <https://doi.org/10.1111/ele.12686>.
- Sinervo, B., Mendez-De-La-Cruz, F., Miles, D.B., Heulin, B., Bastiaans, E., Villagrán-Santa Cruz, M., Lara-Resendiz, R., Martínez-Mendez, N., Calderón-Spinosa, M.L., Meza-Lázaro, R.N., Gadsden, H., Javier-Avila, L., Morando, M., De La Riva, I.J., Sepúlveda, P.V., et al., 2010. Erosion of lizard diversity by climate change and altered thermal niches. *Science* 328, 894–899. <https://doi.org/10.1126/science.1184695>.
- Stahlschmidt, Z.R., French, S.S., Ahn, A., Webb, A., Butler, M.W., 2017. A simulated heat wave has diverse effects on immune function and oxidative physiology in the corn snake (*Pantherophis guttatus*). *Physiol. Biochem. Zool.* 90, 434–444. <https://doi.org/10.1086/691315>.
- Stocker, T.F., Qin, D., Plattner, G.-K., Alexander, L.V., Allen, S., K., Bindoff, N., L., Bréon, F.-M., Church, J., A., Cubasch, U., Emori, S., Forster, P., Friedlingstein, P., Gillett, N., Gregory, J., M., Hartmann, D., L., Jansen, E., Kirtman, B., Knutti, R., Krishna Kumar, K., Lemke, P., Marotzke, J., Masson-Delmotte, V., Meehl, G.A., Mokhov, I.I., Piao, S., Ramaswamy, V., Randall, D., Rhein, M., Rojas, M., Sabine, C., Shindell, D., Talley, L.D., Vaughan, D.G., Xie, S.-P., 2013. Technical summary. In: Stocker, T.F., Qin, D., Plattner, G.-K., Tignor, M., Allen, S.K., Boschung, J., Nauels, A., Xia, Y., Bex, V., Midgley, P.M. (Eds.), *Climate Change 2013: The Physical Science Basis. Contribution of Working Group I to the Fifth Assessment Report of the Intergovernmental Panel on Climate Change*. Cambridge University Press, Cambridge, United Kingdom and New York, NY, USA.
- Telemeco, R.S., Elphick, M.J., Shine, R., 2009. Nesting lizards (*Bassiana duperreyi*) compensate partly, but not completely, for climate change. *Ecology* 90, 17–22.
- Telemeco, R.S., Fletcher, B., Levy, O., Riley, A., Rodríguez-Sánchez, Y., Smith, C., Teague, C., Waters, A., Angilletta Jr, M.J., Buckley, L.B., 2017. Lizards fail to plastically adjust nesting behavior or thermal tolerance as needed to buffer populations from climate warming. *Glob. Change Biol.* 23, 1075–1084. <https://doi.org/10.1111/gcb.13476>.
- Theisinger, O., Berg, W., Dausmann, K.H., 2017. Compensation of thermal constraints along a natural environmental gradient in a Malagasy iguanid lizard (*Oplurus quadrimaculatus*). *J. Therm. Biol.* <https://doi.org/10.1016/j.jtherbio.2017.01.005>.
- Thorpe, R.S., Barlow, A., Malhotra, A., Surget-Groba, Y., 2015. Widespread parallel population adaptation to climate variation across a radiation: implications for adaptation to climate change. *Mol. Ecol.* 24, 1019–1030. <https://doi.org/10.1111/mec.13093>.
- Tolley, K.A., Makokha, Houniet, D.T., Swart, B.L., Matthee, C.A., 2009. The potential for predicted climate shifts to impact genetic landscapes of lizards in the South African Cape Floristic Region. *Mol. Phylogenet. Evol.* 51, 120–130. <https://doi.org/10.1016/j.ympev.2008.11.017>.
- Tyllanakis, J.M., Didham, R.K., Bascompte, J., Wardle, D.A., 2008. Global change and species interactions in terrestrial ecosystems. *Ecol. Lett.* 11 (12), 1351–1363.
- Uetz, P., Freed, P., Hošek, Jiri (Eds.), 2017. The Reptile Database. (Accessed 11 January 2018). <http://www.reptile-database.org>.
- Ujvari, B., Shine, R., Luiselli, L., Madsen, T., 2011a. Climate-induced reaction norms for life-history traits in pythons. *Ecology* 92, 1858–1864.
- Ujvari, B., Shine, R., Madsen, T., 2011b. How well do predators adjust to climate-mediated shifts in prey distribution? A study on Australian water pythons. *Ecology* 92, 777–783. <https://doi.org/10.1890/10.1471.1>.
- Valenzuela-Ceballos, S., Castañeda, G., Rioja-Paradela, T., Carrillo-Reyes, A., Bastiaans, E., 2015. Variation in the thermal ecology of an endemic iguana from Mexico reduces its vulnerability to global warming. *J. Therm. Biol.* 48, 56–64. <https://doi.org/10.1016/j.jtherbio.2014.12.011>.
- Viechtbauer, W., 2010. Conducting meta-analyses in R with the metafor package. *J. Stat. Softw.* 36, 1–48.
- Wang, Y., Zeng, Z.G., Li, S.R., Bi, J.H., Du, W.G., 2016. Low precipitation aggravates the impact of extreme high temperatures on lizard reproduction. *Oecologia*. <https://doi.org/10.1007/s00442-016-3727-x>.
- Wang, Z., Ma, L., Shao, M., Ji, X., 2017. Are viviparous lizards more vulnerable to climate warming because they have evolved reduced body temperature and heat tolerance? *Oecologia*. <https://doi.org/10.1007/s00442-017-3979-0>.
- Wapstra, E., Uller, T., Sinn, D.L., Olsson, M., Mazurek, K., Joss, J., Shine, R., 2009. Climate effects on offspring sex ratio in a viviparous lizard. *J. Anim. Ecol.* 78, 84–90. <https://doi.org/10.1111/j.1365-2656.2008.01470.x>.
- Weatherhead, P.J., Sperry, J.H., Carfagno, G.L.F., Blouin-Demers, G., 2012. Latitudinal variation in thermal ecology of North American ratsnakes and its implications for the effect of climate warming on snakes. *J. Therm. Biol.* 37, 273–281. <https://doi.org/10.1016/j.jtherbio.2011.03.008>.
- Wei, T., Simko, V., 2017. R Package "corrplot": Visualization of a Correlation Matrix (Version 0.84). Available from <https://github.com/taiyun/corrplot>.
- Westphal, M.F., Stewart, J.A.E., Tennant, E.N., Butterfield, H.S., Sinervo, B., 2016. Contemporary drought and future effects of climate change on the endangered blunt-nosed leopard lizard, *Gambelia sila*. *PLoS One* 11, e0154838. <https://doi.org/10.1371/journal.pone.0154838>.
- Whitfield, S.M., Bell, K.E., Philippi, T., Sasa, M., Bolaños, F., Chaves, G., Savage, J.M., Donnelly, M.A., 2006. Amphibian and reptile declines over 35 years at La Selva, Costa Rica. *Proc. Nat. Acad. Sci.* 104, 8352–8356. <https://doi.org/10.1073/pnas.0611256104>.
- Yousefkhani, S.S.H., Aliabadian, M., Rastegar-Pouyani, E., Darvish, J., 2017. Predicting the impact of climate change on the distribution pattern of *Agamura persica* (Dumeril, 1856) (Squamata: gekkonidae) in Iran. *Belg. J. Zool.* 147, 137–142. <https://doi.org/10.24696/bjz.2017.11>.
- Yuan, F.L., Pickett, E.J., Bonebrake, T.C., 2016. Cooler performance breadth in a viviparous skink relative to its oviparous congener. *J. Therm. Biol.* <https://doi.org/10.1016/j.jtherbio.2016.09.003>.
- Yuan, F.L., Freedman, A.H., Chirio, L., LeBreton, M., Bonebrake, T.C., 2018. Ecophysiological variation across a forest-ecotone gradient produces divergent climate change vulnerability within species. *Ecography* 41, 1–11. <https://doi.org/10.1111/ecog.03427>.
- Zani, P.A., 2008. Climate change trade-offs in the side-blotched lizard (*Uta stansburiana*): effects of growing-season length and mild temperatures on winter survival. *Physiol. Biochem. Zool.* 81, 797–809. <https://doi.org/10.1086/588305>.



**Luisa M. Diele-Viegas** is a Ph.D. candidate at the Ecology and Evolution Graduate Program in State University of Rio de Janeiro, Rio de Janeiro, Brazil. She received her B. S. in Zoology at the Federal University of Rio de Janeiro, and her M.S. in Zoology at the Federal University of Pará, in association with the Museu Paraense Emílio Goeldi. Her primary research interests include the influence of climate changes on biology, ecology and distribution of Squamates, and the definition of priority conservation areas for those species.



**Carlos Frederico D. Rocha** has a Ph.D. in Science (Ecology) obtained at Universidade Estadual de Campinas, Campinas, São Paulo, Brazil in 1992. He is Associate Professor at Universidade do Estado do Rio de Janeiro (UERJ) in Rio de Janeiro, Brazil. His main interests are in Ecology and conservation of amphibians and reptiles. He was in the coordination of the Graduate Program in Ecology and Evolution of UERJ from 2008 to 2016 and he is Level I-A Researcher (Higher level of Brazilian scientists attributed by the Brazilian Council of Science and Technology – CNPq) of the Brazilian Environmental Ministry.